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SIMULATED BROWSING IMPACTS ON ASPEN SUCKERS' DENSITY,
GROWTH, AND NUTRITIONAL RESPONSES

by

Koketso Tshireletso

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

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2008

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ABSTRACT

Simulated Browsing Impacts on Aspen Suckers' Density,
Growth, and Nutritional Responses

by

Koketso Tshireletso, Doctor of Philosophy

Utah State University, 2008

Major Professor: Dr. John C. Malechek
Department: Wildland Resources

Heavy and repeated ungulate browsing on reproductive suckers has limited trembling aspen (*Populus tremuloides* Michx.) regeneration on many Western landscapes. However, little is known about the specific effects of season and intensity of browsing. My objectives were to determine the effects of season and intensity of clipping (simulated browsing) on suckers' (1) density and growth characteristics, and (2) nutritional quality and quantity.

Three randomly selected stands were clear-felled in mid-July, 2005, and fenced. Simulated browsing treatments of 0%, 20%, 40%, and 60% removal of current year's growth were randomly applied in early, mid-, and late summers of 2006 and 2007. Sucker density, height, leader length, twig numbers, bud numbers, basal area, and biomass harvested were monitored in each quadrat. Harvested material was analyzed for crude protein and in vitro true dry matter digestibility.

Early summer clipped suckers suffered no winter mortality compared to mortalities of 41% and 42% for mid- and late summer clipped suckers, respectively. However, even at the highest mortality, there were still ample numbers of suckers for stand regeneration. Sucker height was restricted by all early summer treatments. Clipping at 20% and 40% in mid- and late summer, respectively, did not reduce sucker height, but suckers clipped 60% were ≤ 40 cm shorter than controls. Twig and bud density both declined with increasing intensity of clipping. By the study's end, basal area of early summer clipped suckers was higher than for those clipped in late summer.

Crude protein of clipped biomass decreased with season's advance and clipping intensity. Levels ranged from 12.8% to 22.9% and 10.6% to 16.5% in 2006 and 2007, respectively. Digestibility ranged from 80.1% to 93.4% and 75.2% to 90.7% in 2006 and 2007, respectively. Biomass (260 vs. 181 kg/ha) and total digestible dry matter (197 vs. 142 kg/ha) harvested were higher in mid-summer clipped plots in 2007 than in 2006, respectively. Apart from early summer, total nitrogen harvested was not affected differently by season of clipping.

Clear-felling programs that allow browsing of $\leq 40\%$ in mid- and late summer would ensure sustained aspen stand density and growth.

(184 pages)

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to Dr. John C. Malechek for his guidance, and constructive criticism during the course of this study. Appreciation is also extended to Dr. Dale L. Bartos for his advice and consultation on aspen ecology. My thanks also go to Drs. David L. Coppock, Ronald J. Ryel, and James N. Long for guiding my academic program and for serving on my graduate committee.

My greatest appreciation goes to my mother, Mrs. Jenamo Tshireletso, who has been instrumental in my life since childhood. Mother, you are the reason why I see each day worth living. May every day bring happiness for the great mentoring work you have afforded me throughout my life. This work is living memory of your encouragement to find hope in pursuing education. Appreciation is also extended to my siblings, Boijesu, Tjiyapo, Tapedza, Tjengelani, Tjashingwa, and Baboni, and my nephews and nieces. Guys you contributed to my success in many possible ways. It would be unjust if I forgot to express my appreciation to my wife, Phodiso Tshireletso. Dear, this work is dedicated to you for your support.

My appreciation to Morgan Christensen, Clint Stonecipher, Walker Wood, Jordan Wood, Maureen Stewaart, Cade B. Davis, and Seith R. Ohms, for helping in the clearing and fencing of the study sites. Guys keep up the good work.

Lastly, my utmost appreciation goes to my sponsor and employer, Botswana College of Agriculture and Utah State University Agricultural Experiment Station for affording me the opportunity and support for my studies at Utah State University.

Koketso Tshireletso

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CHAPTER 1

INTRODUCTION

Trembling aspen (*Populus tremuloides* Michx.) is the most geographically widespread tree in North America (Barnes 1966; Jelinski and Cheliak 1992; Mitton and Grant 1996; Bartos and Campbell 1998b; Stevens et al. 1999). It is considered a keystone species in the West and one of the best integrators of overall ecosystem health (Bartos and Campbell 1998b). Western forests dominated by trembling aspen are highly regarded by most resource managers for their ability to provide a variety of benefits. They are noted to be beneficial for production of wildlife habitat, scenic beauty, livestock forage, sustaining biodiversity, and they are a potentially valuable source of wood products. For example, aspen stands have been found to contain the highest species abundance and diversity in the West, aside from riparian areas (Bartos and Campbell 1998b). Aspen systems protect the watersheds in which they grow by controlling soil erosion and retaining groundwater that is subsequently made available for stream flow and plant growth (Gifford et al. 1984; Bartos and Campbell 1998b). The loss of aspen from Western landscapes results in an undesirable modification of the regional water budget (Bartos and Campbell 1998b), a resource critically important to the Great Basin region.

Recognition of aspen's decline on Western landscapes has been widely documented (e.g., Smith et al. 1972; Bartos and Campbell 1998a; Campbell and Bartos 2001; Hessler 2002; Hessler and Graumlich 2002). Though the factors contributing to this decline are varied and difficult to separate (Kay and Bartos 2000), it has been partly attributed to excessive browsing by ungulates (Sampson 1919; Smith et al. 1972; Collins

and Urness 1983; Kay 1997; Bartos and Campbell 1998a; Kilpatrick and Abendroth 2001; Shepperd et al. 2001). For example, studies on long-term grazing exclosures have revealed that browsing by native and domestic ungulates hindered aspen regeneration throughout south-central Utah (Kay and Bartos 2000). However, though ungulate browsing is an established cause of poor success in aspen regeneration, beyond that fact, very little is known about the particulars of the response, especially how it is affected by intensity and season of browsing.

In general, the literature is lacking with regard to the role of intensity and season of herbivory impacts on aspen growth and survival. I know in general that herbivory on most plant species can be most detrimental at the early and late season depending on the amount of plant tissue removed (Garrison 1963; Cook 1971; Bergström and Danell 1987). During the early stages of growth, plants invest much of their root stores of energy resources to carry out physiological processes required by the recently-dormant plant. At this stage the plant cannot satisfy all its metabolic demands through current photosynthesis. Though root carbohydrate reserves do not influence aspen sucker initiation, they are important to sucker growth early in development when the photosystem is not fully functional (Frey et al. 2003). Therefore, herbivory during this early part of the season constraints the plant. During the late growing season, the plant requires adequate energy before entering dormancy (Cook and Stoddart 1960; Cook 1971; Willard and McKell 1978). This energy is used for over-winter bud maintenance and to resume growth when conditions are sufficient in the following spring. Essentially, for the plants to tolerate herbivory, they have to withstand the challenge of annually

losing and replenishing these resources. Thus, appropriate timing and level of browsing are critical for the health of plants to ensure growth, development, and survival.

Research has long documented that aspen can tolerate some level of browsing (Julander 1937; Campa et al. 1992). For example, Julander (1937) carried out a clipping study over a 4-year period on the Kaibab National Forest in Arizona and found out that aspen reproduction will deteriorate if 75 percent or more of the current year's sucker growth material is removed. He observed that clipping aspen at 65 to 70 percent removal levels would permit fair growth, but greater growth would occur under lighter clipping levels. Aspen was found to be a key forage species for deer on summer ranges on the Kaibab National Forest. Though this study gave some perspective on aspen response to browsing, it did not compare the effects at different seasons. On another note, Bailey et al. (1990) stated that defoliating aspen in early fall apparently (a) stimulated shoot primordial to grow too late in the season to permit development of winter hardiness, and (b) prevented shoots which had emerged earlier in the growing season from going into dormancy, leaving them susceptible to winter kill. Dockrill et al. (2004) researching the effects of summer cattle grazing on aspen stem injury, mortality, and growth in Alberta, Canada, observed that continuous June-July browsing was the most detrimental time for herbivory to occur in impeding aspen regeneration. This is the time when nutrient resources are at their maximum in the foliage and at their lowest in the perennial tissues (Alban 1985).

As noted earlier, very little is known about the particulars of response of aspen to different levels of herbage removal. I know from browsing studies of various other shrub species that herbivory tends to favor increased production of plant biomass because of

broken apical dominance, leading to opening up of more buds. I also know that heavy browsing tends to favor a shrubby growth form and reduced plant height. However, I do not know at what levels and season herbivory favors these growth mechanisms in aspen, or if they come at a cost that might be manifested as reduced survival of individual suckers. Though these particulars of response of aspen to different levels and season of herbage removal have not been established, Smith et al. (1972) noted that those aspen suckers that escaped terminal leader browsing could establish themselves as adult stems if they attained at least 1.5 m in height. Thus, in light of the available knowledge on aspen and other woody plants' tolerance mechanisms to herbivory, for purposes of the study, I hypothesized that herbivory reduces plant fitness (defined as the ability to attain or surpass the height of at least 1.5 m), and fitness decreases with increasing browsing intensity.

From a browse management standpoint, aspen is considered a major food item for ungulates (especially native ones) in North America. While this may sound contradictory to the overall objective of aspen restoration, the reality of the matter is that substantial use is made of aspen suckers by deer, elk and livestock across the West. This has been specifically documented by several researchers (e.g., Lucas 1969; Bailey and Whitham 2002; Kaye et al. 2005; Davis 2007). However, I know very little about the nutritional value of aspen browse to ungulates. But I know that crude protein and digestibility of plant material usually decrease as the growing season progresses (Kubota et al. 1970; Palo et al. 1985) and as the intensity of clipping increases (Cook and Harris 1968). Studies have demonstrated that early summer browsing decreased nitrogen concentration in leaves of browsed trees in the following summer, while late summer browsing had the

opposite effect, and the effect lasted for at least one year (reviewed by Danell et al. 1994). From the standpoint of the herbivore, these changes have important nutritional implications. For aspen systems where multiple resource use is of interest, it would be appropriate for resource managers to be able to relate the effects of herbivory in terms of energy gain to herbivores and what the plant might tolerate. Therefore, changes in plant traits, for example, crude protein, digestibility, or plant biomass, have direct consequences for the browsing herbivores. Literature is lacking with regard to the relationship of total digestible dry matter removed through herbivory and subsequent biomass production and plant survival. But, I know that biomass removed constitutes a loss of essential nutrients necessary for subsequent plant growth and development. Removing these essential assimilates can obviously not be tolerated indefinitely as represented by an increasing intensity of clipping.

The research questions asked were: (1) Does intensity and season of simulated browsing influence the response (mortality, growth) of aspen suckers? (2) What is the effect of that simulated browsing event (season and intensity) on the quality (crude protein, in vitro true digestibility) of browse material available to herbivores? (3) What is the effect of that simulated browsing event (season and intensity) on the amount of biomass, total digestible dry matter, and total nitrogen that herbivores will be able to harvest in kg/ha? To address the research questions, a controlled simulated summer browsing study was conducted on aspen suckers. Therefore, the objectives and the accompanying hypotheses of the study were:

1. To determine the effects of simulated browsing at four intensities and three seasons on aspen sucker density changes.

Hypothesis 1 (a). I hypothesized that clipping in late summer exposed suckers to winter kill the most, as compared to early- and mid-summer clipping.

Hypothesis 1 (b). I also hypothesized that increased intensity of clipping would be most detrimental to sucker survival over the winter.

Hypothesis 1 (c). Clipping is more detrimental to sucker survival when done in the first growing season compared to the second growing season.

2. To determine the effects of simulated browsing at four intensities and three seasons on aspen growth responses.

Hypothesis 2 (a). Early summer clipping limits plant growth responses the most, compared to mid- and late-summer clipping during the first growing season.

Hypothesis 2 (b). Clipping limits sucker growth responses more as the intensity of clipping increases.

Hypothesis 2 (c). Clipping limits sucker growth the most when done in the first growing season compared to the second growing season.

3. To determine the effects of intensity and season of clipping aspen suckers on the potential nutritional benefit to browsing herbivores.

Hypothesis 3 (a). Crude protein content decreases as the season progresses and as the intensity of clipping increases.

Hypothesis 3 (b). In vitro true digestibility decreases as the season progresses and as intensity of clipping increases.

4. To determine the extent of total digestible dry matter removed that can be sustained by aspen suckers in the next growing season.

Prediction. I predicted that there is a level of biomass removed that can be sustained while still permitting subsequent biomass production.

CHAPTER 2

LITERATURE REVIEW

Herbivory Tolerance Mechanisms of Plants in General

Woody plants often have characteristics that allow them to tolerate some level of browsing and yet also have varying degrees of defense against browsing animals (Bilbrough and Richards 1993). The debate that herbivory benefits plants has been ongoing for decades (reviewed by Belsky 1986). A number of research studies have been published, and are still being published on this theory, with varying conclusions on the role of herbivory effects on plants. Some studies have demonstrated that removal of herbivores led to disappearance of certain plant species from the landscape (McNaughton 1986), a phenomenon leading some to believe that herbivory benefits plants. Others have attributed this phenomenon to competition for resources, especially for short stature species being out- competed by taller species (Belsky 1986). Though well conducted competition field experiments are limited, herbivory may enhance competitive fitness of certain species, particularly graminoids, (Belsky 1986; McNaughton 1986), by opening gaps and promoting co-existence of many plant life-forms.

Woody plants' growth is mediated and controlled by hormonal mechanisms that tend to suppress other growing points while maintaining apical dominance (Haukioja and Koricheva 2000). When apical dominance is broken due to herbivore browsing or other external factors, more buds are likely to open up and initiate growth. These mechanisms that regulate plant re-growth are basically the same as those of normal growth (Haukioja and Koricheva 2000). Woody plants' canopies expand through regulated growth of

individual shoot modules, with those plant parts getting the best access to the resource being favored (Haukioja and Koricheva 2000). These growth mechanisms have been studied and demonstrated in a variety of woody species.

Some researchers have noted that a plant may respond to herbivore attack via escape (Boege and Marquis 2005), avoidance (Milchunas and Noy-Meir 2002), tolerance, induced defense (Gadd et al. 2001; Boege and Marquis 2005), and/or compensation (Gadd et al. 2001). Tolerance has been defined as the ability of a plant to withstand and survive damage (Haukioja and Koricheva 2000; Gadd et al. 2001; Boege and Marquis 2005). Plant escape, defense, and tolerance are likely to vary with plant ontogeny, given the differences in physiological constraints and the selective pressure of herbivores during plant development (Boege and Marquis 2005).

Some studies have documented woody plants producing increased biomass after experiencing grazing (Dangerfield and Modukanele 1996; Rooke 2003; Fang et al. 2006). For example, Belsky (1986) noted that some plants (graminoids) are believed to respond to herbivory by replacing lost somatic or reproductive tissue over-and-above what was lost to the herbivores. These mechanisms, variously described as compensation (increased tissue growth after loss to herbivory), under- and over-compensation (Belsky 1986; McNaughton 1986; Guillet and Bergström 2006), have been studied in woody plants in recent decades. This conceptual framework has also been described as the herbivore optimization hypothesis. The hypothesis asserts that at low or moderate grazing intensity or biomass removal, the plant may be stimulated to make up for, or produce well above the lost tissue amount. However, after a certain level of tissue removal the plant can no longer compensate, leading to under-compensation. Plant

developmental stage and timing when herbivory occurs greatly affects the plant's response (Dyer 1975; McNaughton 1983), a response most likely explained by the mere size of the plant. Bigger plants have a more developed photosynthetic machinery to better withstand some level of herbivory, compared to young, small plants.

The mechanisms that lead to compensatory growth of plants following herbivore damage are complex and interrelated (Dyer 1975; McNaughton 1983). These mechanisms involve changes in physiology and development, and/or modification of the environment (McNaughton 1983). Partial defoliation can result in an increase in light-saturated photosynthesis in the remaining leaves (Dyer 1975; Detling et al. 1979; McNaughton 1986). This increase in photosynthesis is associated with a rapid increase in carboxylating enzymes in both C_3 and C_4 plants (Hewett and Wareing 1973). High cytokinin levels may cause this induction of photosynthetic machinery (Hewett and Wareing 1973; Dyer 1975), and since roots are an important site of cytokinin synthesis (Hewett and Wareing 1973), the movement of cytokinins from roots to residual tissue may be a major mechanism allowing plants to compensate for tissue removal (McNaughton 1983). Other research findings suggest that older senescent leaves may be rejuvenated substantially following defoliation, the result of which appears to be reduced stomatal resistance of remaining leaves (Detling et al. 1979).

Herbivory alters nutrient cycling in plants. Reduced competition for substrates within the plant may stimulate growth of remaining tissues (Dyer 1975). In some instances, increased retention of remaining fruits, greater seed set and larger seeds may follow herbivory on a plant and reduce potential deleterious effects of that tissue removal (McNaughton 1983). On the other hand, shading of lower leaves as the canopy develops

results in gradual decline in their potential physiological activity that is finally accompanied by senescence (Dyer 1975; McNaughton 1983). Prevention of shading can prolong the lifespan of leaves considerably (Belsky 1986; McNaughton et al. 1988). Therefore, defoliation may prolong the active lifetime of productive tissue on the herbivore-affected plant (McNaughton 1983). Though these may be some explanatory mechanisms, responses to herbivory vary greatly among plant species (Bilbrough and Richards 1993).

Mixed findings have been reported as to the response of woody plants in terms of replacement of lost tissues to herbivory, or simulated browsing (Belsky 1986, 1987). To that end, Belsky (1986) noted that the ambiguity of the term compensatory growth has been a major confounding factor in the debate about whether herbivory increases or decreases plant productivity and fitness. As a result, the term has been mis-appropriately used to describe the responses of plants to herbivory. Though, the mechanisms of woody plants response to herbivory have been studied extensively in recent decades, problems still exist as to what currency best describes the possible mechanisms of compensatory growth (Belsky 1986). According to Belsky (1986) the term compensatory growth has also been used in the past to refer to aboveground biomass alone, or to number of shoots, leaves, inflorescences, or seeds. Some studies have noted the lack of compensatory growth in woody plants (Belsky 1986), to some extent due to use of in-appropriate indicator. For example, use of reproductive organs as an indicator to assess compensatory growth in woody plants could easily under-estimate compensation for lost tissue. Woody plants have been observed to delay reproductive activity until they have acquired adequate biomass to sustain reproduction. Belsky (1986) argues that plant

biomass is the best indicator to assess compensatory growth. Plant biomass is cumulative and can be followed from one season to the next unlike other plant traits that can change abruptly with prevailing conditions.

According to Haukioja and Koricheva (2000), woody plants, unlike herbaceous plants, have a long life span and, as such, may need several seasons before compensatory growth is realized. To that end the authors assert that there is no reason to believe that woody plants are any different from herbaceous plants in their ability to compensate for lost tissues. One characteristic feature of woody plants that has been shown to determine or influence compensation for lost tissue is their growth rate (Haukioja and Koricheva 2000). Fast growing woody plants can over-compensate for lost tissues within a short period of time (Guillet and Bergström 2006), compared to slow growing plants.

The mechanisms of plant response to herbivory are plastic, and varied under different environmental conditions (McNaughton 1986; Maschinski and Whitham 1989; Lindroth 2001), demonstrating a continuum of plant responses to herbivory. According to Maschinski and Whitham (1989), herbivory can be detrimental, of no consequence, or even beneficial, depending on the conditions governing a plant's ability to replace tissue consumed by herbivores. The degree of compensatory growth is influenced by timing (Cook 1971; Gdara et al. 1991), and intensity of grazing (Cook 1971; Gdara et al. 1991), nutrient (Hemming and Lindroth 1999; Maschinski and Whitham 1989) and water availability (Maschinski and Whitham 1989), history of herbivory or defoliation (Gdara et al. 1991; Bowyer and Neville 2003; Thorne et al. 2005), and type (Thorne et al. 2005; Guillet and Bergström 2006) and age of tissue eaten (Guillet and Bergström 2006). Collectively, these factors influence a plant's physiological state and its ability to

compensate for herbivory (Maschinski and Whitham 1989). Plants in high resource environments are thus most likely to respond positively to lost tissues compared to the same species under poor environmental conditions (Belsky 1987; Bartolome 1993; Relva and Sancholuz 2000). Plants growing in poor nutrient environments have been observed to invest more resources into defense rather than tolerance mechanisms when they are injured (McKey 1974; Sagers and Coley 1995), a move that appears logical to defend the remaining and developing young plant parts.

Even though plant tolerance to herbivory has been demonstrated in a wide range of woody species, very little is known about the mechanisms that defoliated aspen display under natural conditions. I know that herbivory has been asserted as one of the factors that hinders aspen regeneration (Bartos and Campbell 1998a; Kay and Bartos 2000), but little is known about aspen's tolerance to herbivore browsing, especially as affected by season, and intensity of defoliation. Very few studies have attempted to study the effects of herbivory impacts on aspen, especially concerning timing (Carson et al. 2007), and intensity (Julander 1937; Campa et al. 1992; Osier and Lindroth 2004) of defoliation. Given the vast knowledge on other woody plants' response to tissue removal, one would think that there are response mechanisms to herbivory that can be extended to the aspen issue. However, given the clonal, and inter-connected nature of aspen, it remains to be seen how aspen responds to different seasons, and intensities of defoliation. Tolerance is considered to be an especially viable form of defense in plants with high intrinsic growth rates, large storage capacity, and substantial physiological (e.g., photosynthetic) plasticity, all traits that are characteristic of aspen (Lindroth 2001). However, it remains to be seen how these mechanisms play out in aspen suckers. Therefore, this review on

plant tolerance mechanisms to herbivory formed the theoretical framework, for the current research.

Herbivory Studies on Woody Plants

There are not many studies that have been done on simulated browsing on aspen. However, several clipping studies have been conducted on other woody species browsed by big game and range livestock. Hence, there might be some general principles that can be inferred from similar studies done on other woody species. The following is a review on response and tolerance mechanisms displayed by other woody plants due to tissue removal.

Herbivory tolerance by plants is varied among woody plant species. In a 4-year clipping study on the Kaibab National Forests, Julander (1937) observed that cliffrose (*Cowania stasburiana*) clipped so that more than 80% of its current year's growth increment was removed, deteriorated, while removal of 70 to 75% was the maximum amount which permitted recuperation and perpetuation of cliffrose. He also observed that removal up to 65% was beneficial in stimulating growth of cliffrose.

Cook and Stoddart (1960) conducted a 3-year study on desert sagebrush in central Utah to determine how sagebrush (*Artemisia tridentata*) responded to two different types of herbage removal. One treatment involved removing one-half of the current growth of each twig over entire plant and the other was removing all of the current year's growth from only one-half of the plant. They observed that clipping all of the current year's growth from one side of the plant during late winter or early spring caused death of that one-half of the plant after 3 years of treatment. On clipping one-half of all current year's

growth over the entire plant, vigor of the plant was reduced substantially, but only small isolated twigs or branches were killed. They also concluded that there is little or no translocation of manufactured food from one side of the plant to the other.

Defoliation at certain time periods can be more or less detrimental to plant growth and development than at other times. Early summer defoliation can be most detrimental to plants, because of limited carbohydrate reserves to support growth. A 4-year study on the Fremont, Malheur, and Whitman National Forests in Oregon, and the Snoqualmie National Forest in Washington (Garrison 1963) investigated the effects of clipping current twig growth at 25% (lightly clipped), 50% (moderately clipped), 75% (heavily clipped) and 100% (completely clipped) on five range shrub species. He recommended levels of use for sustained shrub production on winter ranges in Oregon and Washington: for antelope bitterbrush (*Purshia tridentata*) on best sites, 60 to 65%, and 50% on poorer bitterbrush sites; for snowbrush ceanothus (*Ceanothus velutinus*), 35 to 40%; for rubber rabbitbrush (*Chrysothamnus nauseosus*), 50%; for creambush rockspirea (*Holodiscus discolor*), 50 to 60%; and for curlleaf mountainmahogany (*Cercocarpus ledifolius*) plants completely within reach of grazing animals, 50 to 60%. However, he cautioned that the information in this study should be applied only to fall and winter ranges, suggesting differential responses to season of use.

A 12-year clipping study was conducted in southwestern Colorado on long-term effects of yearly removal of specific amounts of current-annual-growth (CAG) stems and older material from five locally important browse species: antelope bitterbrush, big sagebrush, oakbrush (*Quercus gambelli*), mountain mahogany (*Cercocarpus montanus*) and serviceberry (*Amelanchier alnifolia*) (Shepherd 1971). Treatments included annual

clippings of 20, 40, 60, and 80% of the CAG stems for 12 years and 100% for 10 years. Shepherd concluded that for serviceberry, annual use of up to 60% of the CAG stems, 1 centimeter or more in length, would be beneficial, but that sustained use of 80% or more would be harmful and eventually kill the plants. For oakbrush, a 60% utilization of CAG on summer and fall ranges was found to be optimum use, while for mountain mahogany browsing intensity of approximately 70% proved optimum. It was observed that summer and fall use of bitterbrush CAG stems in amounts of 20 to 40% promoted plant health and vigor. He also noted that 50% use might be acceptable, but a sustained use of 80% or more would eventually damage or kill many plants. Though the study demonstrated that big sagebrush maintained high browse production under clippings of 20 to 80%, greater proportions of dead branches and plants were noted. Therefore, it was concluded that summer and fall use in excess of 50% could not be tolerated for an indefinite period.

Willard and McKell (1978) conducted a 5-year study in the Wasatch Mountains of Utah within the Cache National Forest, a typical summer range for cattle, to investigate the effects of simulated browsing on little rabbitbrush (*Chrysothamnus viscidiflorus*) and snowberry (*Symphoricarpus vaccinioides*) shrubs at light (30%), moderate (60%) and heavy (90%) intensities of twig and leaf removal during early (1 June), mid- (15 July), and late season (1 September). They observed that 30% herbage removal produced an increase in herbage production while more intense defoliation usually caused a decrease in both species. Twig length was reduced on little rabbitbrush shrubs but not on snowberry.

A 2-year study was conducted southwest of Grand Rapids, Minnesota, to study the effects of overstory and understory competition and simulated white-tailed deer (*Odocoileus virginianus* Zimmermann) herbivory on growth and survival of white pine (*Pinus strobus* L.) seedlings (Saunders and Puettmann 1999). Treatments involved three intensities of clipping (control, 0% previous year's growth removed; lightly clipped, terminal and 50% previous year's growth removed, and heavily clipped: 100% of previous year's growth removed) and three frequencies (never clipped, clipped once, clipped 2 years in a row). They observed that decreasing overstory canopy closure and brush competition generally increased growth of seedlings under all clipping regimes, with heavy clipped seedlings showing the least benefit of reduced competition. On the other hand, they also observed that seedling mortality was higher without brush control and after clipping. Since both competition levels and increased herbivory reduced seedling vigor, they concluded that understory brush control and deer protection go hand-in-hand to regenerate white pine.

Puettmann and Saunders (2001) conducted a later 2-year study in the same area to study, patterns of compensatory growth of eastern white pine seedlings as influenced by simulated herbivory intensity and competitive environments. Treatments included, an unclipped control or the removal of the terminal and approximately 25%, 50%, 75%, or 100% of last year's shoots. Seedlings were grown with different understory competition levels (created through monthly weeding vs. no brush control) under a range of overstory canopy closures. It was noted that after one growing season, seedlings did not fully compensate for lost biomass, regardless of competitive environments of the seedlings. They also observed that, though relative height growth was stimulated by light intensity

(20-40% of last-year shoots removed), relative diameter growth, total biomass, and biomass growth of seedlings declined sharply with increasing clipping intensity. On the other hand, all growth parameters declined with increasing inter-specific competition. It was observed that seedlings in highly competitive environments showed smaller growth loss due to clipping than those in competition-free environments. They attributed this to the fact that, seedlings experiencing high inter-specific competition devoted more energy to maintaining apical dominance and a balanced shoot-root ratio. They concluded that compensatory growth follows a complex pattern that will vary with the parameters measured, competitive conditions, and clipping intensities. They also noted that overcompensation maybe an adaptation to competitive ability, rather than a response to herbivory itself.

In another study, Maschinski and Whitham (1989) examined the single and interactive effects of plant association, nutrient availability, and timing of herbivory by rock squirrels (*Spermophilus variegatus* grammurus) and mule deer (*O. hemionus*) on the relative fitness of an herbaceous biennial, *Ipomopsis arizonica* (Polemoniaceae) under natural conditions. To determine plant association with herbivory, plants growing with proximity with other plants were selected. To examine the interaction of water and nutrient levels with herbivory and/or plant association, plants were supplemented with water and fertilizer; treatment combinations were (1) water and fertilizer, (2) water, or (3) control (no water or fertilizer). To determine how early- and late-season herbivory influenced fruit set and compensatory ability, between-year differences and within-year differences of clipped-plant response were used. They observed that the probability of compensation for herbivory decreased as competition with other plants increased, as

nutrient levels decreased, and as the timing of herbivory came later in the growing season. This study demonstrated the plastic (continuum) responses of plants under different environmental conditions.

In general, herbivory is assumed to cause a significant loss of plant growth, survival and fecundity (Tuomi et al. 1994). Browsing by large mammals may strongly constrain the growth of woody plants (Herder et al. 2004), and the response may vary between different growth stages. Herder et al. (2004) studied the effects of summer browsing (levels not specified) by reindeer on the growth of willow (*Salix phylicifolia*), by studying plants inside and outside exclosures over a period of 6 years. They concluded that reindeer browsing in summer reduces height of willow, shoot length, biomass, and diminishes reproductive success, and accelerates dieback of shoots of browsed willow more than unbrowsed willow.

Ungulate browsing may cause a variety of morphological and physiological changes in plants, which depend on browsing intensity and frequency, the type of herbivory and time of the year when browsing occurs (Thorne et al. 2005; Guillet and Bergström 2006). For example, late winter browsing by moose (*Alces alces*) resulted in an increase in diameter at the point of browsing on twigs that had been browsed previously over twigs re-growing from second-year growth that had not been browsed (Bowyer and Neville 2003). Guillet and Bergström (2006) studied the effect of timing and intensity of simulated deer browsing on compensatory response by fast growing willow (*Salix viminalis*) grown for bioenergy in south Sweden. Seasons of clipping were mid-June (early summer), mid-July (mid summer), mid-August (late summer), and January (winter). Intensities were 25%, and 100% of all twigs clipped. It was observed

that willows compensated for biomass losses after winter clipping, irrespective of clipping intensity, whereas total biomass production usually decreased after high intensity summer clipping. The higher the proportion of twig biomass removed by summer clipping, the lower the compensatory growth by willow, demonstrating the differential response of plants to browsing. In another study, Bergström and Danell (1987) studied the effects of 25%, 50%, 75%, and 100% clipping intensity on morphological and biomass response of two birch plants (*Betula pendula* and *B. pubescens*). Increased clipping intensity resulted in decreased long-shoots numbers, the frequency of branched shoots increased, the basal diameter length and dry weight of individual shoots decreased, and the number of buds increased, but total number of buds on all current annual long-shoots decreased. Height and main stem diameter decreased with clipping intensity.

Plants can respond differently to browsing depending on their browsing history (Bowyer and Neville 2003). Thorne et al. (2005) studied the response of two groups of willow plants (*Salix planifolia* var. *planifolia* Prush) with different clipping histories. Clipping events comprised of all possible combinations of early, middle, and late season periods, with clipping frequencies 1, 2, and 3 times. Willow production was influenced by the accumulation of specific combinations of seasonal clipping events and was dependent on clipping history of the plants. Early season clipping, alone or in combination with other events, was more detrimental to willows with prior clipping histories than middle or late season clipping treatments. The phenological stage of a plant is important in browsing management. Browsing tends to reduce the photosynthetic surface area, thus constraining plant growth and development. As noted earlier,

defoliating in early season can be most detrimental to the plant because the plant's photosynthetic surface area is not fully developed to replace lost tissues to defoliation.

A major challenge in evolutionary ecology is to describe the evolutionary response of plants to damage by herbivores (Stowe et al. 2000; Stinchcombe 2002). These evolutionary responses to damage include resistance and tolerance traits. Some plants have been observed to produce or invest more in defense mechanisms than growth when browsed (McKey 1974; Tuomi et al. 1994; Sagers and Coley 1995). Veraart et al. (2006) studied the effects of pruning willow (*Salix dasyclados* Wimm.) on use by beaver (*Castor fiber* L.) in and after the following growth season. They observed that beavers browsed willows that were pruned earlier in the growing season compared to those that were pruned later in the growing season. They concluded that their findings suggested that willows invest in compensatory growth rather than a defense response early in the re-growing phase compared to late growing season.

Aspen Responses to Herbivory

Quaking aspen is a long-lived clonal species in which many genetically identical stems (i.e. ramets) arise from a common root system (Day 1944; Barnes 1966; Schier 1976; Bartos and Mueggler 1981, 1982; Bartos et al. 1991). Romme et al. (2005) used manipulative experiments to investigate the patterns and mechanisms of new aspen genet establishment, growth, survival during their first decade of development in Yellowstone National Park. Treatments included (1) clipping current year's growth to simulate browsing, (2) removal of potential competitors and herbaceous plants, (3) clipping with competitor removal, and (4) control, i.e., no treatment except protection from browsing.

These authors reported reduced stem elongation from clipping current year's growth, and removing potential competitors had no significant effect on height growth of aspen seedlings. Even with protection from browsing, most aspen stems grew slowly (mean increment < 25 cm from 1996 to 2000), and many died from causes un-related to herbivory.

Herbivory on aspen has been observed to hamper growth and regeneration (Kilpatrick and Abendroth 2001). Impacts of wild and domestic herbivory on aspen suckers following fire treatments can be adverse and may quicken the demise of clones (Bartos and Mueggler 1981; Bartos et al. 1991; Amacher et al. 2001). Bailey and Whitham (2002) reported a decrease in aspen regeneration on sites that had previously burned severely compared to sites that had intermediate burns. Elk utilized the severely burned site because of differential high sucker densities compared to the intermediate burned site. In the Central Rocky Mountains, Kaye et al. (2005) also reported a greater than 50% decline in mean sucker recruitment for stands highly browsed by elk.

Lucas (1969) studied the effects of cattle, sheep, and other factors on aspen reproduction after clear-cut logging in southern Utah. He observed that sheep utilized more suckers than cattle, and survival of aspen suckers was 10% greater under protection from grazing than under livestock grazing. He also observed that first year suckers were very susceptible to over-browsing because of their short height and high palatability. The first year following cutting is critical to successful aspen regeneration, for that is the year when most of the suckers emerge (Smith et al. 1972). However, increased height and woodiness of suckers during the second and third years made suckers more resistant to livestock damage (Lucas 1969). Cattle utilize aspen suckers more readily late in the

season than early (Fitzgerald et al. 1986), because of the maturation and consequent coarsening of associated herbaceous plants with season advance.

In another study, Smith et al. (1972) evaluated the effects of deer and domestic livestock on aspen regeneration at several sites in Utah. They observed that where livestock were present together with deer, utilization and terminal bud removal of aspen were substantially greater (ranging from 17-31%) than where domestic livestock were absent. Excessive use of aspen suckers was not observed when sheep or cattle grazed for short periods even though stocking rates were heavy.

The effect of short duration, long term heavy grazing by cattle on associated herbaceous plants was evaluated after burning and seeding of an aspen grove at the University of Alberta, Canada (Bailey et al. 1990). The objective of the grazing treatments was to remove all accessible edible material, and kill the aspen. Early (June) or late (August) season grazing reduced the density of aspen, and reduced its height, preventing the development of a forest canopy. According to Bailey et al. (1990), defoliation in early fall apparently (1) stimulated shoot primordia to grow too late in the season to permit winter hardiness, and (2) prevented shoots which had emerged earlier in the growing season from going into dormancy, leaving them susceptible to winter kill.

Kay and Bartos (2000) assessed long-term exclosures in late summer of 1995 and 1996 to determine aspen stem dynamics in the Dixie and Fishlake National Forests in south-central Utah. The exclosures consisted of a three-part design with a total-exclusion portion, a livestock-exclusion portion, and a combined-use portion which permitted the effects of deer and elk herbivory to be measured separately from those of livestock. Stem densities were 1,012, 2,498, and 4,474 stems/ha for the combined wildlife-livestock-use

plots, livestock-exclusion-plots, and total-exclusion-plots, respectively. This study gave some indication on the effects of herbivory on aspen sucker survival.

In another study, Bartos et al. (1994) reported aspen sucker densities 12 years post fire treatment ranging from 1,500 to 2,400 stems/ha, which was 29 to 38% less than pre-burn densities. The control also had a 39% decrease in number of suckers, which was attributed to elk use. Kilpatrick and Abendroth (2001) also reported a significant difference ($P < 0.05$) in mean stem height of 1.4 m on northeast aspects compared to 0.80 m on south-southwest aspects. The authors attributed the difference in mean stem height between aspects to differential browsing by ungulates.

The effect of cattle on aspen regeneration was evaluated by determining the effect of no grazing, June-only grazing, July-only grazing, and continuous June-July grazing on aspen height and density (Dockrill et al. 2004). Continuous June-July grazing impeded aspen regeneration relative to the control (no grazing). This is the time when minimal nutrients are in the perennial tissues of aspen (Alban 1985). A decrease in the number of suckers per hectare typically occurs as a consequence of natural thinning during the first five years after the adult trees have been harvested (Bartos and Mueggler 1981; Bartos et al. 1991). Dockrill et al. (2004) observed that aspen stem mortality within June-July and June grazing plots were approximately 200% and 50% greater than that of the ungrazed plots, respectively. Cumulative stem mortality in the ungrazed plots over the duration of the experiment was approximately 12%, which is presumed to reflect natural thinning rate (Dockrill et al. 2004). Therefore, the authors attributed the reduction in aspen stem density for the grazing treatments to the effects of cattle.

The effects of defoliation on plant growth can persist into several growing seasons following the defoliation event (Osier and Lindroth 2004; Stevens and Lindroth 2005). Measurement of plant characteristics allows for evaluation of long-term genetic variation in tolerance to defoliation (Lindroth 2001; Osier and Lindroth 2004). Osier and Lindroth (2004) grew saplings of four aspen genotypes in a common garden under two conditions of nutrient availability, and subsequently subjected them to two levels (0% and 100% leaf area removed) of artificial defoliation. Genetic and environmental factors and their interactions could play important roles in affecting plant's response (Stevens and Lindroth 2005) to defoliation. However, Osier and Lindroth (2004) observed that artificial defoliation suppressed plant growth, but saplings of the four genotypes did not show evidence of genetic variation in tolerance to defoliation. Though these findings give some perspectives on herbivory tolerance of aspen, I do not know how the same set of saplings would perform under natural conditions.

Regeneration Mechanisms of Aspen

Aspen is a clonal species that regenerates via suckering after disturbance removes or kills partially or all of the aboveground portions of the clone (Schier 1976; Jones et al. 1985a; reviewed by Frey et al. 2003). Abundant root suckering is thought to be important for ensuring the successful re-establishment of vigorous aspen stands after disturbance (reviewed by Frey et al. 2003; Fraser et al. 2004). Aspen suckering has been thought to be controlled by hormones especially auxins which are produced in the crown of trees and transported to the roots and subsequently maintain apical dominance (Schier and Campbell 1978; Schier and Campbell 1980). Though this has been (and still is) the

working theory, other researchers have noted that it is not the only mechanism that explains root suckering in aspen following disturbance (Schier 1976, 1982; reviewed by Frey et al. 2003). Frey et al. (2003) in a synthesis paper have also questioned hormonal influences as the only mechanism regulating aspen regeneration. Some studies have demonstrated that though hormones play a part in aspen regeneration and growth following disturbance, season of logging, genetic variation (Frey et al. 2003), and other environmental factors are also important (Schier 1976; Frey et al. 2003). Warmer temperatures have been observed to promote aspen regeneration (Schier 1976, 1982). Auxins that are responsible for suppressing suckering are believed to be unstable and destroyed at high temperatures, resulting in the breaking of apical dominance (Schier 1976). In general, thousands of suckers are usually produced following a major disturbance like clear-fell-coppice (Bartos and Mueggler 1982), so long as live root system exists prior to the disturbance (Ohms 2003).

Climatic Variability and Aspen Regeneration

Aspen has the largest ecological amplitude of all tree species in North America (Barnes 1966; Jelinski and Cheliak 1992; Mitton and Grant 1996; Bartos and Campbell 1998b; Stevens et al. 1999; Appendix A, Fig. A). This wide geographic adaptability has allowed the species to persist across landscapes for generations (Barnes 1966). According to Campbell and Bartos (2001), aspens may have survived past climatic variations and persisted on these sites. However, climatic fluctuation in recent decades has been implicated to the decline of aspen in the West (Frey et al. 2003). It is hard though to single out climate change as a driving mechanism to the decline of aspen.

Though drought may cause aspen decline on some landscapes, other studies have documented no apparent relationship between climate variability and the decline of aspen (Romme et al. 1995, 2005; Kay and Bartos 2000). Other studies have documented that aspen regeneration is limited to asexual reproduction in the Intermountain West (Baker 1925; Day 1944; Barnes 1966; Bartos and Mueggler 1981, 1982; Bartos et al. 1991), suggesting minimal seedling recruitment in the region (but see Genetics section below). The explanation to this phenomenon has been that the region rarely experiences ideal conditions necessary for aspen seedling establishment.

Disturbance, Stand Age, and Aspen Regeneration

Research has documented that clearcutting and prescribed burning stimulates abundant root suckering (Bartos and Mueggler 1981, 1982). Disturbances such as clearcuts modify factors such as light and temperature that may enhance sucker production (Lavertu et al. 1994). Canopy opening permits light infiltration to the soil surface, thus increasing soil temperature and promoting sucker initiation (Schier 1976; Bartos and Mueggler 1981). The amount of suckering often depends on the degree of disturbance, provided that the stand is not breaking up due to old age and decay (Mueggler 1989; Ohms 2003).

Lavertu et al. (1994) studied the effects of stand age and litter removal on regeneration of aspen on six sites of different ages (46, 74, 120, 143, 167, and 230 years since last fire) at Lake Duparquet in NW Quebec, Canada. They observed that the number of suckers produced did not differ along the successional sere for any of the three years studied. It was also observed that mortality after three growing seasons was about

60% for all plots and was not affected by seral stage and treatment. As a result of competition for space and nutrients, self thinning was high (Lavertu et al. 1994). Aspen sucker numbers follows a negative exponential decay curve, with mortality highest in the first five years following disturbance (Bartos et al. 1991). Mueggler (1989) also reported that sucker numbers were unrelated to the amount of under-growth, stand basal area, or stand age in the Intermountain West.

Aspen Genetics, Regeneration and Herbivory

Species with life history characteristics similar to aspen (an outcrossing breeding system, large geographic range, long-lived, high fecundity, and wind-dispersed pollen and seeds) often have high levels of genetic diversity (Jelinski and Cheliak 1992; Mitton and Grant 1996; Stevens et al. 1999; Madritch et al. 2006). However, it is widely believed that sexual reproduction is rare in populations of aspen in the Intermountain West (Baker 1925; Moss 1938; Barnes 1966), due to limiting environmental conditions. Recent research findings have since modified this widely held hypothesis (Jelinski and Cheliak 1992; Stevens et al. 1999; Quinn and Wu 2001; Romme et al. 2005). A variety of genetic and other evidence indicates that recruitment of new genets through sexual reproduction has occurred infrequently throughout the Holocene, during brief windows of opportunity when seed availability and suitable climatic and substrate conditions combined to provide the very exacting requirements for germination and survival of aspen seedlings (Jelinski and Cheliak 1992; Mitton and Grant 1996). For example, Quinn and Wu (2001) recently reported aspen regeneration from seed after a stand replacing fire in the Chiricahua Mountains of southeastern Arizona. In another study,

Shepperd et al. (2006) have also reported considerable genetic diversity within local populations, and even within stands in some places. In Yellowstone National Park, Romme et al. (2005) reported seedling occurring but with little establishment after the historic 1988 wild fire. Fire breaks down canopies and releases competition from other vegetation (Kay 1993; Hessl 2002), thus enabling an environment suitable for seedling establishment.

Genetic variation in aspen presents a potentially interesting interactive effect with herbivory. Differential use by herbivores on neighboring aspen stands has been observed on landscapes in southern Utah (Winter 2008). This then raises the question of whether genetic variation can explain differences in use by herbivores (Wooley et al. 2008). On this note, one begins to wonder if the responses of aspen to different clipping intensities would differ among individual suckers of different genetic make-up.

Carbohydrates, Nitrogen, and Plant Growth

Carbohydrates and nitrogen are the major constituents for plant growth and development (Orodho and Trlica 1990; Forwood and Magai 1992; Lacey et al. 1994; Morvan-Bertrand et al. 1999). These carbohydrates and nitrogen are important assimilates that the plant uses for metabolic processes needed for growth and development (Mandre et al. 1998). Essentially, for the plants to tolerate herbivory, they have to withstand the challenge of losing and replenishing these resources.

Research on herbaceous plants has long documented the importance of carbohydrate reserves for plant growth following defoliation (Krueger and Bedunah 1988; Reece et al. 1988; Lacey et al. 1994; Donkor et al. 2003). In a root sprouting study

on aspen, Tew (1970a) reported an increase in root carbohydrate reserves of more than 5% from June to September in one growing season. The increase was attributed to an increase in photosynthetic area as the growing season advanced. Adequate carbohydrate reserves at the time of disturbance and rapid development of leaf area by extensive sprouting after disturbance seem critical for resilience of the clone. These two factors facilitate retention of the clonal root system and a rapid rebuilding of carbohydrate reserves (Landhäusser and Lieffers 2002). Landhäusser and Lieffers (2003) assessed the changes in seasonal carbohydrate status, including sugar and starch concentrations in roots, stem xylem and phloem, and branches of 10 different clones of trembling aspen in Alberta, Canada. They observed that carbohydrates are stored as close as possible to the organs of annual growth (e.g., leaves and buds), suggesting significant stress to the plant with defoliation events because of removed energy. Starch and sugar reserves in most tissues were very low in early summer (Landhäusser and Lieffers 2003), suggesting that defoliation at this time may hamper subsequent plant growth. However, it has been pointed out that a decrease in the amount of non-structural carbohydrates did not necessarily imply causal role for these reserves in initiating and affecting re-growth (Morvan-Bertrand et al. 1999). Though root carbohydrate reserves do not influence sucker initiation, they are important to sucker growth early in development when the photosystem is not fully functional (reviewed by Frey et al. 2003).

Seasonal Variation in Nitrogen in Plants

Trembling aspen is a major food item for many ungulates in North America (Ullrey et al. 1964; Kubota et al. 1970; Kufeld 1973; Schwartz et al. 1988), and its

nutritional composition warrants further assessment. While this may sound contradictory to the overall objective of aspen restoration, the reality of the matter is, substantial use of aspen suckers by elk, and deer in Arizona (Bailey and Whitham 2002; Kaye et al. 2005), and sheep on Cedar Mountain (Lucas 1969; Davis 2007) has been reported. Though the nutritional composition of aspen has been reported in several studies (e.g. Ullrey et al. 1964; Kubota et al. 1970; Tew 1970b; Kufeld 1973; Alban 1985; Schwartz et al. 1988; Jelinski and Fisher 1991), very little research has been done linking such forage dry matter removed by herbivory (or simulated browsing) and subsequent biomass production. Therefore, this section is a review of aspen from the standpoint of its nutritional value to herbivores, with special emphasis on nitrogen and dry matter digestibility, and their seasonal variation.

Wild ungulates populations, e.g., deer, can be limited by quality and less by quantity of forages available to them (Chen et al. 1998). Dry matter digestibility and nitrogen are common measures of forage quality (Tew 1970b; Chen et al. 1998). Fulfillment of the energy requirements of ungulates is strongly influenced by the digestibility of the forages they consume, since apparent digestibility of dry matter and energy are strongly correlated (Chen et al. 1998).

The factors influencing the nutritive value of range forages are many, and the degree to which they are interrelated may vary considerably from one area to another (Short et al. 1966). However, the stage of growth (level of maturity) seems to be the most important factor affecting chemical composition and digestibility (Oelberg 1956). In general, all forages are highly succulent in early growth, and their high protein content in relation to a low fiber content at this stage makes them highly nutritious (Oelberg

1956). Despite the over-riding influence of maturity, edaphic and climatic influences can also affect the nutritive value of forages (Oelberg 1956; Cook 1971). Climatic factors affect respiration, assimilation, photosynthesis, and metabolism to the extent that the mineral and organic matter content of plants may be strongly modified by micro climatic differences even though growing on the same soil (Oelberg 1956).

Important seasonal changes occur in the chemical composition of leaves as well as of twigs of woody plants and probably reflect the combined effects of advancing maturity and changing environmental conditions (McHargue and Roy 1932; Tew 1970b). Protein content of browse tends to decrease as the season advances (Palo et al. 1985). As a rule, crude protein is low in winter twigs, it increases in spring, and then reaches a maximum in early summer (Palo et al. 1985). During the growing season, nitrogen levels are high ($> 1.5\%$) only during the short period when leaves of browse are available for browsers (Kubota et al. 1970). During this period the percentage of crude protein ranges from about 10% to 20% before it becomes uniformly low (6 % to 8%) for the remainder of the year (Kubota et al. 1970). Previous studies have documented that young leaves have more protein than old leaves (McHargue and Roy 1932; Tew 1970b; Chapin and Kodrowski 1983), a pattern that appears evident for the reviewed literature on aspen nutrition (Table 2.1). Crude protein levels tend to be high for aspen earlier in the summer growing months, a period of active photosynthetic surface area of young and developing leaves.

Research has documented that nutrients are re-translocated between senescing leaves and perennial tissues in deciduous trees (Chapin et al. 1975; Bartos and DeByle 1981; Chapin and Kedrowski 1983; Alban 1985; Chapin and Moilanen 1991; Killingbeck

Table 2.1. Literature reports of seasonal mean crude protein (%) content for woody species, with special emphasis on trembling aspen (*Populus tremuloides* Michx.).

Species	Months of the year												Location	Citation
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec		
	-----Crude protein (%)-----													
<i>Salix planifolia</i>						17	13	8.8	-	-	-		Colorado	Baker & Hobbs 1982
Willow (<i>Salix spp</i>)	8.9	8.5	9.2	-	-	-	-	-	-	-	-	8.4	Canada	Morgantini and Hudson 1985
Aspen (leaves)	3.39	-	-	3.72	-	-	3.14*	-	-	3.63	-	-	South Dakota	Gastler et al. 1951
Aspen (leaves)	-	-	-	-	9.4	16.3	13.1	-	6.3	-	-	-	Alaska	Kubota et al. 1970
Aspen (leaves)	-	-	-	-	-	17.0	13.2	-	11.8	-	-	-	Utah	Tew 1970b
Large toothed aspen (sprouts)	5.0	-	-	-	-	-	-	-	-	-	-	-	Michigan	Ullrey et al. 1964
Aspen (leaves & twigs)	-	-	-	-	-	-	-	-	-	13.6	-	-	Michigan	McCullough 1979
Aspen (leaves & twigs)	-	-	-	-	-	8.8	-	-	-	-	-	-	Washington	Mould & Robbins 1981
Aspen (leaves)	-	-	-	-	31.25	-	-	-	12.5	-	-	-	Minnesota	Alban 1985
Aspen (twigs)	-	8.4	-	-	-	-	-	-	-	-	-	-	Michigan	Campa et al. 1992
Large toothed aspen (twigs)	-	8.5	-	-	-	-	-	-	-	-	-	-	Michigan	Campa et al. 1992

Aspen (*P. tremuloides* Michx.); Large toothed aspen (*P. grandidentata*); * Aspen stems

1996; Milla et al. 2004). This re-translocation process may partly explain why seasonality of nutrients in certain plant parts is evident in some tree species. Chapin and Kedrowski (1983) followed concentrations of nitrogen seasonally in leaves and young stems of four Alaskan tree species: larch (*Larix laricina*), black spruce (*Picea mariana*), birch (*Betula papyrifera*), and alder (*Alnus crispa*). They reported high nitrogen levels in young leaves across species, followed by declines in concentration through the season. Seasonal nutrient concentration changes in the perennial tissues e.g., bark are often as large as for the foliage in aspen (Alban 1985), demonstrating the movement of these nutrients between senescing leaves and perennial tissues. According to Alban (1985), these changes are largest in the spring and autumn, but substantial changes also occur in mid- summer.

Due to diverse genetic variation of trembling aspen, one can only imagine that nutrient variations within and among clones are a possibility. Clonal variation in chemical composition has potentially important implications for vertebrate herbivores because a single clone may be large and thereby, comprise a large part of available forage (Jelinski and Fisher 1991). Jelinski and Fisher (1991) examined (1) the spatial variability in nutrient concentrations (2) and evaluated these differences with respect to elk and deer nutritional requirements, within and among 24 clones of trembling aspen, at Water Lake National Park, Alberta, Canada. Between-clone concentrations of all chemicals were significantly different, with crude protein limiting in some clones for elk and deer protein requirements. Mean crude protein concentration ranged from 4.56% to 7.44% and averaged 6.25%. Most clones were observed to meet the protein requirements for wintering maintenance of elk (5 to 7%) (Ullrey et al. 1967; Mould and Robbins 1981).

Protein requirements for adult deer are believed to range from 6 to 9%, a range that is adequate for ruminal bacterial digestion (Van Soest 1982; Demment and Van Soest 1985). According to French et al. (1956), protein requirements for growth are considerably higher ranging from 12 to 16%. Jelinski and Fisher (1991) reported that only one clone fell beneath the minimum protein requirements for elk, but eight clones fell below the minimum threshold for deer. These clonal chemical composition differences may have implications for cervid nutrition.

Seasonal Variation in Dry Matter Digestibility in Plants

Low forage digestibility may seasonally limit vertebrate populations on some landscapes (Chen et al. 1998). In vitro dry matter digestibility (IVDMD) differs greatly among forages (Robbins and Moen 1975; Robbins et al. 1975), and generally decreases as the growing season advances (Kubota et al. 1970; Palo et al. 1985). It also decreases with increasing levels of utilization (Oelberg 1956), due to an increase in fiber content of the remaining forage material.

Robbins and Moen (1975) reported an average IVDMD of 51.69% for 18 deciduous browse plants, but levels ranged between 42.45% and 62.05% at Ithaca, New York. IVDMD may vary greatly during the year (Table 2.2). Chen et al. (1998) studied IVDMD of forages utilized by wapiti (*Cervus elaphus*) and roe deer (*Capreolus caprolus*) in northeastern India. They reported that IVDMD decreased from 43.8 to 64.3% in spring to 29.4 to 40.5% in winter for wapiti, and from 52.4 % to 77.4% in spring to 25.9 to 36.5% in winter for the roe deer. It was also noted that roe deer had higher IVDMD (40% to 71.7%) in both leaves and twigs of browses than wapiti (35.9%

Table 2.2. Literature reports of seasonal in vitro dry matter digestibility (IVDMD, %) values for woody species, with special emphasis on trembling aspen (*Populus tremuloides* Michx.).

[illegible]

to 58.7%) during snow-free seasons, but IVDMD of twigs was lower for roe deer (25.9% to 36.5%) than wapiti (29.4% to 38.4%) in winter.

CHAPTER 3

MATERIALS AND METHODS

Description of the Study Area

The study area was located on privately owned land on Cedar Mountain at an elevation of 2800 m. The site was approximately 27 km southeast of Cedar City, Utah.

The vegetation consists of interspersed mountain grasslands and woodlands of quaking aspen, with patches of Gambel oak (*Quercus gambelii* Nutt.) (Ohms 2003). Some areas have well defined stands of the shrub, mountain snowberry (*Symphoricarpos oreophilus* Gray). The dominant grasses are Letterman needlegrass (*Stipa lettermani* Vasey), Kentucky bluegrass (*Poa pratensis* L.), with lesser amounts of mountain brome (*Bromus carinatus* Hook & Arn), and slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinn.) (Bowns and Bagley 1986). Forbs are noted to be inconspicuous and considerably less abundant than grasses. Common forbs on the area include western yarrow (*Achillea millefolium* L. var. *occidentalis* DC.), thick-stem aster (*Aster integrifolius* Nutt.), lambstongue senecio (*Senecio integerrimus* Nutt.), dandelion (*Taraxacum officinale* Webber ex Wiggers), knotweed (*Polygonum douglasii* Greene), tarweed (*Madia glomerata* Hook.), and coneflower (*Rudbeckia occidentalis* Nutt). The area has a long history of heavy continuous sheep grazing, and it is postulated that the relatively low abundance of forbs in relation to grasses is the result of this grazing history (Bowns and Bagley 1986). Plant nomenclature follows Welsh et al. (1993).

Precipitation and Temperature Distribution

Mean annual precipitation for Cedar Mountain from a rain gauge located 11.2 km from the study site was 711 mm from 1970 to 2007 (Fig. 3.1A). Precipitation mainly comes as winter snow and as much as one-third from summer monsoons (Ohms 2003). Annual precipitation for the area was 1,323 mm, 640 mm, and 810 mm for 2005, 2006, and 2007, respectively. Growing season precipitation (April to October) averaged 342 mm from 1970 to 2007, whereas in 2005, 2006, and 2007, it averaged 768 mm, 340 mm, and 612 mm, respectively.

Long-term (1992-2007) average temperature ranged from -3.5 °C in January to a day-time maximum of 15.9 °C in July (Fig. 3.1B). Temperature ranges for the years of study were within the limits of the long-term record.

Site Selection

During late spring of 2005, three aspen stands were randomly selected on the Thorley's ranch portion of the larger Cedar Mountain Initiative (Ohms 2003) research area (Fig. 3.2) located at lat 37°29'652''N and long 112°56'247''W. Stands at least 0.4 ha were identified and numbered. Then, stand numbers were written in pieces of paper, folded and put in a hat. The first three numbers drawn comprised the stands used in this study. The stands measured approximately 70 x 70 m in dimension, and were on a fairly straight line on a north to south axis. However, Sites 2 and 3 were located on a gentle north-facing slope compared to Site 1 which was fairly flat.

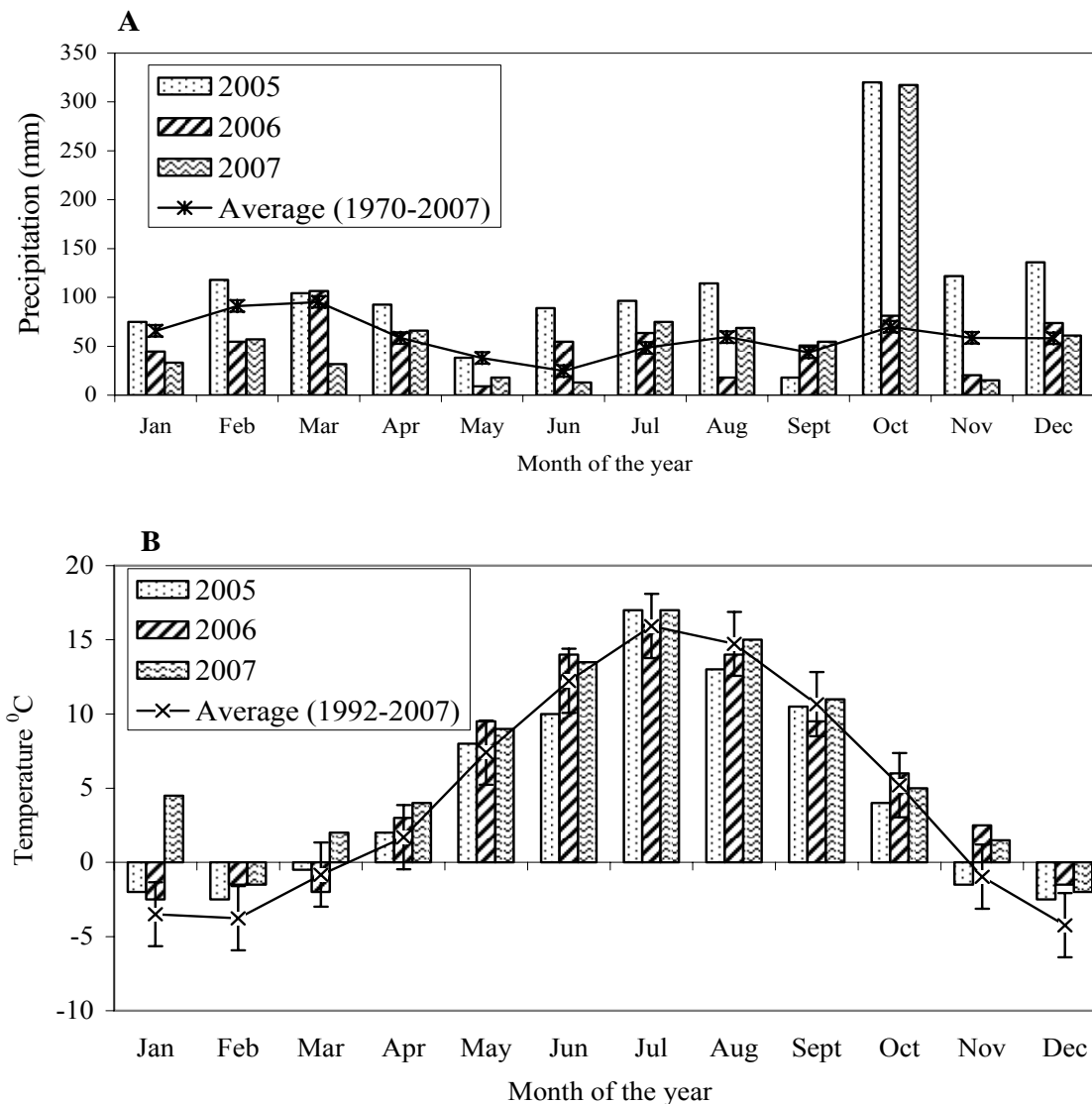


Figure 3.1. Mean (A) monthly precipitation (mm) and (B) monthly temperature ($^{\circ}\text{C}$) for 2005, 2006, and 2007, with long term mean monthly precipitation (1970-2007), and temperature (1992-2007) overlaid. Precipitation data was from a rain gauge located at Southern Utah University College Farm, Cedar City, approximately 11.2 km from the study area (Courtesy of Dr. James E. Bowns, Professor, Southern Utah University). Temperature data were an average from two weather stations located at Kolob and Webster Flat that are roughly equidistant from the study area. Source:

<http://www.wcc.nrcs.usda.gov/snotel/snotel.pl?sitenum=561&state=ut>

<http://www.wcc.nrcs.usda.gov/snotel/snotel.pl?sitenum=853&state=ut>

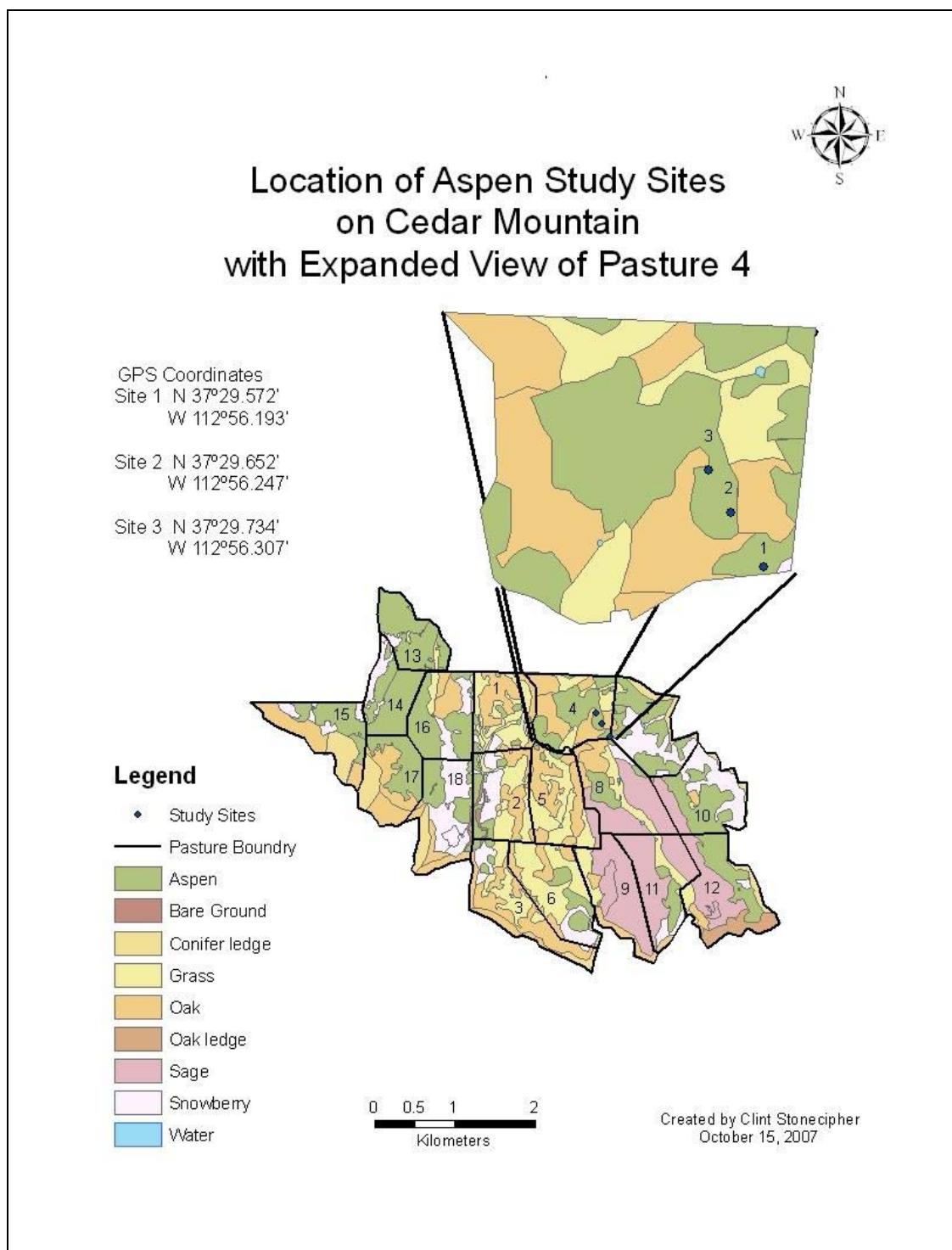


Figure 3.2. Location of research aspen stands on Thorley's ranch with expanded view of Pasture 4 on Cedar Mountain, Utah. The study area was located on a privately owed ranch about 27 km southeast of Cedar City, Utah.

Initial Stand Characteristics

Stem Density. Before clear-felling, aspen stem density was estimated. I achieved this by throwing a survey pin over my shoulder at three randomly selected locations within a stand. The point where the survey pin landed formed the center of a 2- x 30-m belt transect. All aspen stems within the belt transect were counted and expressed as stems/ha. Stem density did not differ statistically ($P > 0.05$) between the three Sites, and averaged (mean \pm SE) $1,500 \pm 468$, $1,833 \pm 468$, and $1,333 \pm 468$ stems/ha for Site 1, 2, and 3, respectively. Research has documented that an aspen clone will likely fail to regenerate successfully and sustain itself if stand density falls below 1,250 stems/ha (Bartos and Campbell 1998a). The stand densities for the current study were well above this limit, indicating that there were, at least, not deteriorating.

Stand Age. Before clear-felling, 10 trees were randomly selected from each site and cross sections were cut at breast height (1.37 m) for average stand age determination. This was achieved by throwing a survey pin over my shoulder into the stand. A tree within two meters of the survey pin was identified and marked. The procedure was repeated until 10 trees were identified and marked. Diameter at breast height (DBH) averaged (mean \pm SE, cm) 38 ± 3 , 20 ± 3 , and 14 ± 1 for Sites 1, 2 and 3, respectively. These samples were then labeled, taken to the laboratory and left at room temperature until they were dry. Tree age was later determined following the procedures described by Asherin and Mata (2001). Cross sections were sanded with sandpaper until annual rings became apparent. Cooking oil was then rubbed on the finely sanded surface to make the annual rings visible for counting. Each cross section was divided into 4 sections with line marks running through the centre. A dissecting binocular was used to aid in counting the

annual rings. The average of the number of rings counted in each of the 4 sections estimated the age of the cross section. Because annual rings were not visible in the center of the cross section due to rotting, four years were added to the total number of annual rings for each tree (Campbell 1981). Estimated average stand age was 104 ± 5 , 65 ± 14 , and 27 ± 3 for Sites 1, 2, and 3, respectively. The oldest trees were 134, 112, and 54 years old for the three respective sites.

Site Preparation and Maintenance

Initially we planned to clear-fell trees as soon as the snow melted in 2005, in order to have a flush of aspen suckers for treatments that year. However, because 2005 was a wet year we could not get to the site until late June, and other logistics of planning, including stand selection, took some time. The selected stands were clear-felled in mid-July of 2005, and logs were immediately hauled off site using a front-loader equipped farm tractor. The operation resembled a commercial harvest (clear-fell coppice) where big logs were removed leaving behind the small branches. Clear-fell coppice and soil disturbance by the tractor ensured sucker stimulation and emergence due to elimination of apical dominance (Schier 1976).

The cleared stands were immediately fenced with a 1.2-m high wire field fence. To that was attached a 3-m high game proof black plastic mesh (Figs. B.1-B.3) to protect suckers from ungulate browsing. The game proof plastic mesh was taken down in late fall of 2005 just before the snow fell to prevent it from being crushed by the snow. The plastic mesh was replaced in late spring of 2006 as soon as the area was accessible by vehicle. I assumed that suckers would remain covered and protected by snow through the

winter, thus incurring minimal browsing during that period. However, because the roads were muddy and impassible long into spring of 2006, substantial amounts of suckers were lost to early spring ungulate browsing. For this reason, the fences were left standing at the end of the growing season in 2006 and over the winter period of 2006-2007. The fences held well over the winter, and minimal repair was required in spring of 2007.

Soil Texture

The soils are generally described as Argic Pachic Cryoborolls, with fine montmorillonitic fair clay loam, with slopes of 0-28% (Bowns and Bagley 1986). However, to determine the uniformity of the sites in terms of soil texture, I collected soil samples in June 2005. Soil samples were collected by throwing a survey pin over my shoulder into the cleared stands. Where the survey pin landed formed a sampling point. This procedure was repeated until four sampling locations were identified and soil samples collected. Soil samples were collected within each site at 15 cm depth and put in soil collection cans. The samples were then taken to the laboratory for soil particle analysis using the hydrometer method (Gee and Bauder 1979, 1986). Site 1 had a sandy loam texture, Site 2 a loam, clay-loam texture, and Site 3 a loam, clay-loam texture (Table C.1).

Soil Water Content (%)

Soil water content fluctuations on the study sites were monitored through the sampling periods in 2007. In late spring of 2007, the study area was visited to check and repair the fences. It was observed through visual assessment that Site 3 appeared to be

relatively drier compared to Sites 1, and 2. I then decided to take soil samples to determine how soil water content changes through the sampling periods. Soil samples were randomly collected at six locations within each site at depths of 15 and 30 cm and put in soil collection cans. This was achieved by throwing a survey pin over my shoulder into the stand, and where it landed formed the sampling point. The procedure was repeated until six samples were collected. Soil water content (%) was determined by the gravimetric method (Gee and Bauder 1986), and the results are shown in Table C.2.

Aspen Genetics¹

To determine the genetic uniformity of the aspen stands, genetic studies were conducted. Duplicate leaf samples were taken at five systematically identified locations on each site for a total of 10 samples per site from the suckers that emerged after the clear-fell coppice treatment. These samples were collected at the end of July 2006. Leaf samples were immediately put in silica gel for preservation. These samples were later taken to the laboratory at Utah State University, Logan, Utah for DNA extraction.

Total genomic DNA was extracted using the Qiagen DNEasy-96 ¹Plant Kit. DNA was amplified across 5 highly polymorphic microsatellite loci: WPMS-14 and WPMS-15 (van der Schoot et al. 2000; Smulders et al. 2001), GCPM-970-1, PMGC-576, and PMGC-2571 (http://www.ornl.gov/sci/ipgc/ssr_resource.htm). Each 10 µL amplification reaction contained: 0.2mM each dNTP, 1x reaction buffer, 1.8 mM MgCL₂, and 0.25 µL each of fluorescently labeled FAM or HEX forward primer and unlabelled reverse primer. An initial denaturation for 2 minutes at 95 °C, was followed by 30 cycles of 94 °C for 30 s, 52-57 °C for 40 s, and 72 °C for 50 s, with a final extension for 10 min. at 72 °C.

¹Genetics expertise of Dr. Karen Mock, USU Wildland Resources, is acknowledged.

Amplification reactions were visualized and analyzed using an ABI 3730 capillary system and GeneMapper v4.0 software (Applied Biosystems, Inc.).

From the analysis of the samples submitted, it was determined that Site 1 was genetically uniform and had identical alleles at all 5 loci (Table C.3). Sites 2 and 3 had two different 5-loci genotypes observed each. Although the study sites shared some genes, overall they were genetically different from each other. Considering the fact that only a limited number of five (x 2 duplicate) leaf samples were collected for each site, more genes would probably have been revealed had the sample size been larger.

Experimental Factors

To study the response of aspen suckers to browsing, a simulated browsing experiment was conducted. Factors included season (3 periods), clipping intensity (4 levels), sampling time (referred to as “Time” in statistical analysis and figures) (2 levels) and year (2006, 2007) and their interactions. Sampling time referred to when measurements were made, i.e., at the beginning of a season before clipping, and at the end of the growing season. Specifically, in this document times B06 and B07 refer to before clipping at each season in 2006 and 2007, respectively. The A06 and A07 refer to the end of the growing season in 2006 and 2007, respectively. Browsing was simulated by clipping at 0%, 20%, 40% and 60% removal of the current year’s growth. Suckers were clipped in early season or early summer (ES; 15 June), mid-season or mid-summer (MS; 30 July) and late season or late summer (LS; 15 September) on the same plots (suckers) in 2006 and 2007. For each season, all clipping was completed within a week to ensure that environmental variability was minimized.

Experimental Layout

In June 2006, each stand was divided into three roughly equal portions. On each of these portions, four transects were established, running the entire length of the fenced stand. These transects were placed such that each one had a buffer zone of at least 2 m from the nearest transect where possible. Before treatments were assigned to these transects, the three portions of the stand were randomly assigned to the three seasons. This was achieved by writing stand portions in pieces of paper, folded and put in a hat. The pieces of paper were drawn one at time, and allocated to ES, MS or LS. Within each of the stand portions, the browsing intensities were also randomly assigned to the line transects. Again the randomization was done as above (in ascending order), with intensity 0% getting the first allocation.

Along each transect, 15 1.0-m² (square shape) permanent quadrats were established utilizing the nearest plant method (USDI 1996; USDA 2004) for monitoring aspen suckers. For this procedure a general direction was chosen by identifying a distant landmark in front of the observer. A transect was then started by taking 2 paces in the direction of the landmark. The nearest sucker within 0.91 m using a 180-degree selection zone in front of the lead boot was identified, marked with a plastic tag and the aspen sucker marked the center of a permanent quadrat. To permanently mark a quadrat, two 1-m white fiberglass electric fence posts were pounded into the ground at opposite corners. These posts were then marked with a permanent marker indicating the clipping season, clipping intensity and quadrat identification. The procedure was repeated until 15 quadrat placements per intensity were located and marked. Where it was not possible to fully utilize the nearest plant method, because of a heterogeneous distribution of aspen

suckers, adjustments were made to slightly deviate from the general transect direction, thus meaning going where suckers were. This was particularly experienced at Site 3, which had un-uniform spread and fewer aspen suckers compared to Sites 1 and 2.

Definition of Terms

In this document twig refers to current year's shoot produced on a sucker (Fig. 3.3). Terminal leader or leader refers to the longest twig that would most likely assume apical dominance. Twig basal diameter and sucker basal diameter refers to the base diameter of a twig, and sucker, respectively.

Measurements

At each quadrat, one sucker was selected and permanently marked for sucker height and terminal leader length measurement. Because most suckers that existed in the summer of 2006 had emerged in the spring and summer of that year, leader length closely approximated sucker heights i.e., leader length was considered as the same as sucker height. Total number of buds, number of current year's twigs, basal diameter of each sucker, and number of suckers (density) were measured at each quadrat. In 2006, the total number of buds was individually counted. However, as the suckers expanded their canopies in 2007, it became very time-consuming to individually count the buds. Therefore, total number of buds was estimated by selecting two twigs and counting their buds. This value was then divided by 2 to give average number of buds per twig. This number was then multiplied by the total number of twigs to give total number of buds at each quadrat. Basal diameter of all suckers was measured at ground level. Height measurements were measured to the nearest 0.5 cm using a 1-m ruler, and basal sucker

and twig diameters were measured to the nearest 0.1 mm using dial calipers. These variables were measured before each treatment session at each season, and again at the end of the growing seasons in October 2006 and 2007.

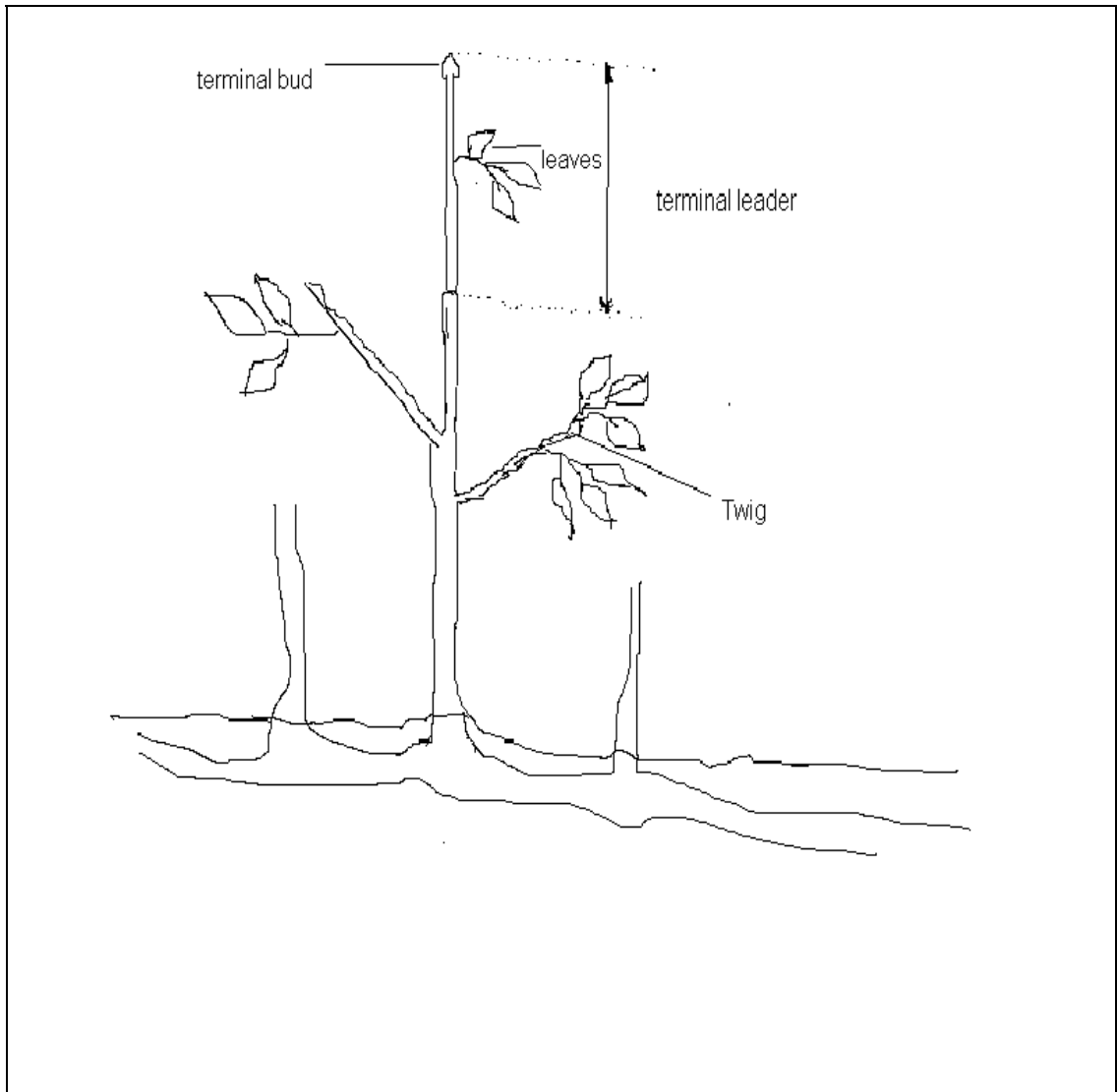


Figure 3.3. Diagram showing the components of an aspen sucker. Terminal leader refers to the longest current year's growth or twig that stands above all and would most likely assume apical dominance. Leaves are only produced on current year's growth i.e., they are only produced on current year's twigs.

Before treatments were imposed, I practiced estimating, followed by clipping and weighing, variable percentage amounts of sucker foliage on off-site plants until a level of consistency was achieved between my estimates and weighed amounts. This followed the ocular estimation method (Bonham 1989). For example, I clipped, 20% of the current year's foliage on a sucker and then weighed it. After that the remaining portion of the sucker was clipped at ground level and also weighed. The initially clipped material was then expressed as a percentage of the total plant weight to see how close it came to the 20% removal intended. Then, at each treatment quadrat, a specified clipping intensity was imposed on the current year's growth of every branch of each sucker, based on my ocular estimates. To minimize the chance occurrence of spreading pathogens between suckers, the hand clippers were dipped into 70% alcohol before a new sucker was clipped. Young aspen suckers are known to be very susceptible to pathogens, especially when they are injured (Harniss and Nelson 1984; Baker et al. 1993; Guyon 2004). However, in this study disease incidence were not observed.

Biomass and Basal Area Estimation

Basal stem or twig diameter measurements were used to estimate current year biomass of suckers (Brown 1976) for each quadrat. The procedure assumes that basal diameter of suckers or twigs are circular in shape, and are predictably related to their biomass. At each season, 50 current year's suckers or current year's twigs outside the experimental area were clipped at the base using a hand clipper, and basal sucker or twig diameters measured. The harvested samples were then taken to the laboratory and oven dried at 70⁰ C for 72 hours and weighed. Linear regression equations for basal sucker

diameter, or basal twig diameter (whichever was applicable) and biomass were then developed for each data set for each season, and at the end of the growing season. The equations took the form of $\ln(\text{biomass, g}) = a + b \ln(\text{basal diameter, cm})$, where \ln was the natural logarithm, a , was the y-intercept, and b was the slope of the line (Table C.4).

Because most suckers that had sprouted in the summer of 2005 were lost to ungulate browsing in early spring of 2006, most suckers that existed in the summer of 2006 had appeared that spring and summer. Therefore, basal sucker diameters were utilized to estimate biomass of suckers prior to imposition of treatments. However, at the end of the growing season in 2006, and again in the summer of 2007 basal diameter of current year's twigs instead of whole plant basal sucker diameters were used to estimate current year's biomass. To estimate current year's average twig diameter per quadrat, two randomly chosen twigs were measured at the base. Their basal diameters were then averaged to get twig diameter, and this value was substituted in the appropriate formula to calculate biomass of the individual twig (Table C.4). This value was then multiplied by the number of twigs to get total current year biomass for the quadrat (see Table C.5 for total biomass for different seasons and intensities).

Basal sucker diameter measurements were also used to calculate basal area of the suckers at each season and end of the growing season. The equation used to calculate basal area was πr^2 , where r was the radius of the base of the sucker, in cm. Basal area of individual suckers, were then summed to give total basal area at each quadrat (cm^2/m^2).

At the end of growing season, all of the experimental units for all seasons were revisited and measurements taken for all the above variables. In addition to the above measurements, the numbers of new suckers were also recorded. The measurements and

treatments were repeated in the summer of 2007. Measurements for all treatments were again taken at the end of the growing season of 2007.

Sample Preparation and Grinding

All of the clipped sucker material was bagged in paper bags in the field. At each sampling time, leaves were also collected from off-quadrat suckers within the enclosure for comparison of nutritional composition of harvested materials. Leaves were collected from suckers without paying any particular attention to location on the sucker. These samples were then taken to the laboratory and oven-dried at 70⁰ C for 72 hours. After drying, the samples were then weighed.

When the clipped samples were very small, composite samples were created by combining the nearest experimental units for each treatment and within a season. All samples were then ground through a Wiley mill (Thomas Scientific, Swedesboro, NJ) equipped with a 1-mm screen. Ground samples were then put in sealed containers until analyzed.

Nutritional Analyses

Dry matter (DM) percentage (so-called “laboratory dry matter”) was determined for each of the intensities for the different seasons. Ground samples (0.5 g) of each treatment (n = 5-8) were weighed into pre-weighed dry crucibles, and placed in an oven at 105 ⁰C overnight (AOAC 1996). Percent DM was calculated as weight of sample after drying divided by sample weight before drying, and then multiplied by 100.

Samples for each treatment (n = 5-8) within a season were analyzed for nitrogen (N) by the combustion method (AOAC 1996) using a nitrogen analyzer (Leco, St. Joseph, MI). Crude protein content (%) was calculated as N x 6.25.

In vitro true digestibility (IVTD) for each treatment (n = 5-8) within a season was determined following the procedures of Tilley and Terry (1963), and Van Soest et al. (1966), utilizing the ANKOM modified procedure (ANKOM Technology Corporation, Fairport, NY). This procedure involved placing 0.25 g of ground dry samples in F57 filter bags. The F57 filter bags were later heat sealed. They were then batch digested in a mixture of a buffer solution (pH 6.8), and rumen liquor (400 ml) placed in a closed Daisy^{II} Incubator for 48 hours, maintained at 39.5 °C. Rumen liquor was obtained from two ruminally-fistulated Angus cows that were maintained on grass hay-alfalfa diet. A standard grass-hay of known digestibility was included with every run. After 48 hours in the Daisy^{II} Incubator, the samples were removed and placed in 4-L beaker. The samples were then rinsed thoroughly with cold tap water using minimal mechanical agitation until water ran clear. After rinsing, the bags were placed in an ANKOM^{200/220} Fiber Analyzer (ANKOM Technology) and processed through the neutral detergent fiber (NDF) procedure. Basically, this procedure substitutes alpha amylase for pepsin in the Tilley and Terry (1963), and Van Soest et al. (1966) procedures. IVTD was then calculated as follows (ANKOM Technology):

$$\%IVTD_{DM} = 100 - ((W_3 - (W_1 \times C_1)) \times 100 / (W_2 \times DM))$$

Where:

W1 = Bag tare weight

W2 = Sample weight

W_3 = Final bag weight after In Vitro and sequential NDF determination.

$C1$ = Blank bag correction (final oven-dried weight/original blank bag weight).

DM = % dry matter (multiply by the decimal equivalent).

Statistical Analyses²

Plant Data Responses. All data for sucker density and growth variables (sucker height, leader length, twig density, bud density, basal area) were analyzed as a 3-way factorial in a split-split plot design with whole plots in blocks with analysis of variance (ANOVA) using the MIXED procedure of SAS (SAS/STAT software, Version 9.1.3 of the SAS System for Windows 2002-2003. Copyright © SAS Institute Inc.; Appendix D for SAS code). Whole plots were stand portions nested within sites (blocks), and the whole plot factor was season (with 3 levels: early, mid-, late summer). Subplots were transects within stand portions, and subplot factor was intensity (4 levels: 0%, 20%, 40%, 60%). Repeated measures on the transects were the sub-subplots, and the sub-subplot factor was time (B06, B07, A06, A07) or year (2006, 2007). Fixed effects included season, intensity, sampling time, or year and their interactions. Sites were considered random effects. For count variables, zero values were included in all analyses because they were legitimate data values. However, for measurement data (basal area, sucker height, and leader length) zero values were treated as missing data in the analyses.

Four analyses of different subsets of the data were performed on sucker density and sucker growth variables (Fig. 3.4). All analyses used the ANOVA model identified above. The first analysis, involved comparison of sucker responses before any treatments were applied in 2006 to 1-year-old suckers in 2007 (termed B06 vs. B07 in text).

² The statistical consultation of Ms. Susan Durham, USU Ecology Center, is acknowledged.

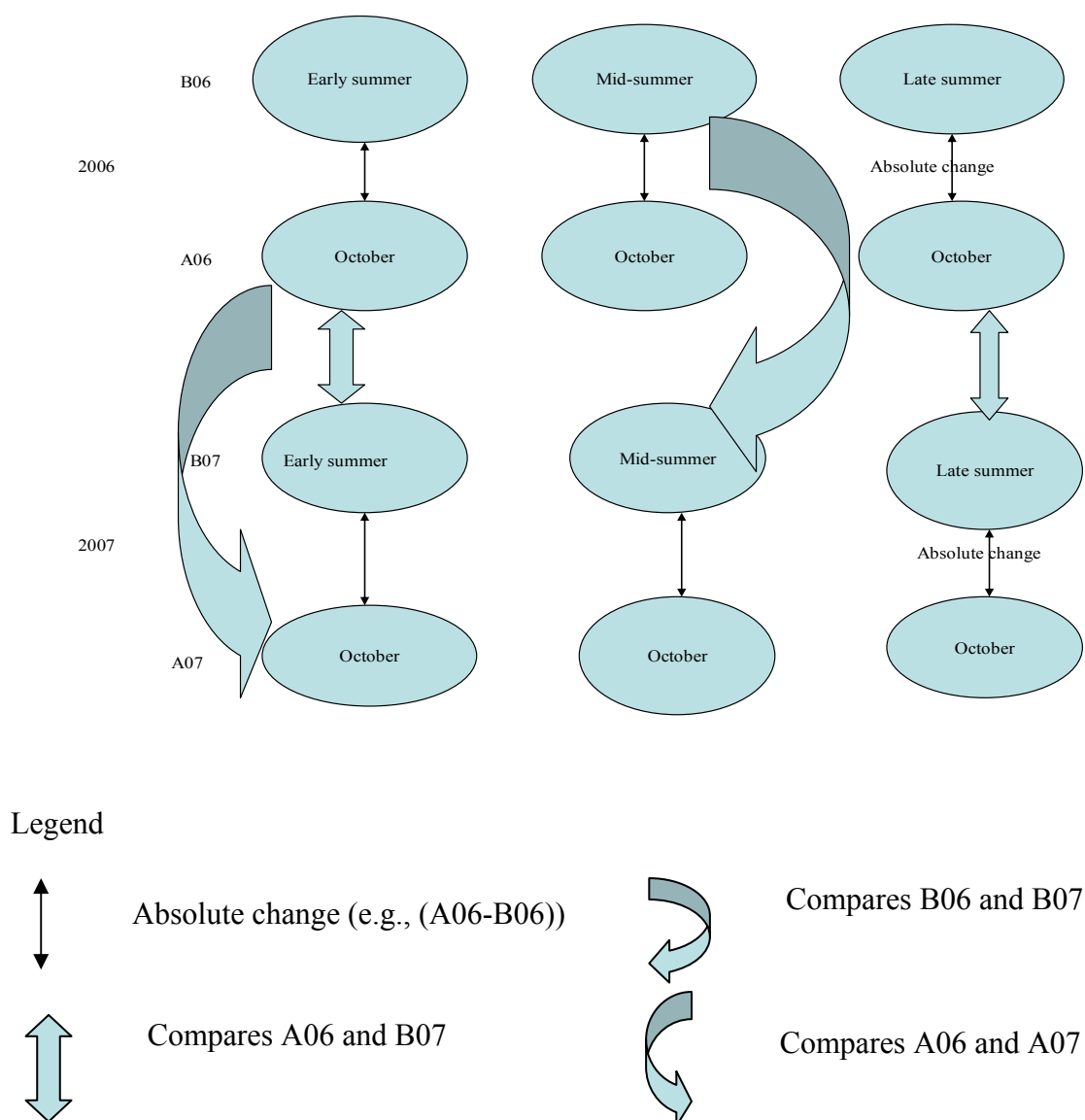


Figure 3.4. Diagrammatic representation showing the time or year comparisons made for the analysis of response variables in the analysis of variance (ANOVA). (1) B06 and B07 compared the initial stand characteristics just before clipping (B06) in 2006 and effects of that initial clipping one year later, just before clipping (B07) in 2007. (2) A06 and B07 time comparison was performed only for sucker density, and it estimated over-winter mortality of suckers. (3) A06 and A07 compared the response of variables at the end of the growing season in 2006, and 2007, respectively. (4) The fourth analysis involved creating a new variable known as change in response variables. This variable was calculated by subtracting values of response variables at the beginning of seasons from values at the end of the growing season for each year. Also, instead of time, year was the new fixed effect variable in the model for ANOVA, for the fourth analysis.

The second analysis compared the sucker density responses at the end of the growing season in 2006 with those of before clipping in 2007 (termed A06 vs. B07 in text). This analysis allowed assessment of over-winter effects (eg., winter mortality) on suckers.

The third analysis compared the sucker responses at the end of the growing season in 2006 and 2007 (termed A06 vs. A07 in text). This analysis allowed comparisons to be made for sucker responses after one clipping event and after two years of consecutive clippings.

The fourth analysis, compared change in sucker responses in 2006 and 2007 (2006 vs. 2007). Change in sucker variables (sucker density, sucker height, leader length, basal area) within a year was calculated by subtracting the value of a variable before any clipping that year from the value at the end of the growing season ([A06-B06] and [A07-B07], for 2006 and 2007, respectively). Additionally, in calculating change for measurement data, there had to be a value before clipping and at the end of the growing season within a year. If any value was zero (because of dead sucker, for example), it was treated as missing in the analysis. Sampling time was replaced by year (2006 vs. 2007) as a fixed effect in the ANOVA model. The analysis allowed comparisons of change for sucker responses after one clipping event and after two consecutive clipping events.

Multiple comparisons of the least square means for the fixed effects were made using the Least Significance Difference (LSD) procedure (Dowdy and Wearden 1991). Differential tests were considered significant at $P < 0.05$. Prior to analysis, all count data were square root transformed and measurement data were log transformed to better meet

the assumptions of homoscedasticity and normality for ANOVA. All means reported herein are descriptive statistics computed using the un-transformed raw data.

Nutritional Data Responses. Crude protein and in vitro true digestibility data were analyzed using the same model described above, with season, intensity, year and their interactions as fixed effects. Sites were again considered random effect in the model.

Biomass, total digestible dry matter and total nitrogen harvested were also analyzed using the same model described above. Total digestible dry matter and total nitrogen harvested were calculated as follows:

Total digestible dry matter harvested = IVTD (%) x biomass harvested

and

Total nitrogen harvested = %nitrogen in harvested material x biomass, respectively.

CHAPTER 4

RESULTS

Effects of Intensity and Season of Clipping on First Year's Sucker Responses

Sucker Density. The season when clipping occurred affected sucker density (Fig. 4.1). Early summer clipping was least ($P \leq 0.014$) detrimental to sucker survival, compared to clipping in late summer. Approximately 45%, 54% and 43% fewer suckers were present in early, mid- and late summer clipped plots, respectively at time B07 than at time B06. These results described a season and time interaction effect for sucker density (Table 4.1).

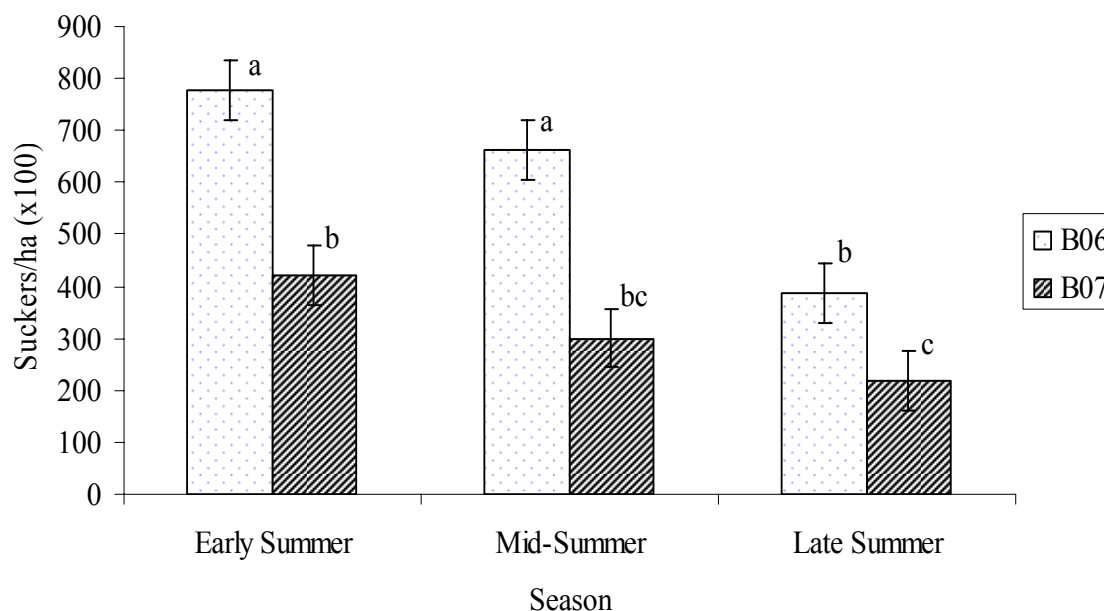


Figure 4.1. Mean comparisons for sucker density before clipping in 2006 and 2007, for three seasons. B06, B07 = before suckers were clipped at the beginning of seasons in 2006, and 2007, respectively. Error bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

Table 4.1. ANOVA fixed effects of season, intensity, and time of clipping on sucker density, sucker height, leader length, current year twigs, bud density, and basal area growth for B06 (beginning of the growing seasons in 2006) and B07 (beginning of the growing seasons in 2007) data.

Source	Num DF	Den DF	F Value	¹ P- Value
Suckers/ha				
Season	2	4	10.65	0.025
Intensity	3	18	1.21	0.334
Season x Intensity	6	18	0.65	0.691
Time	1	24	88.79	<0.000
Season x Time	2	24	2.33	0.119
Intensity x Time	3	24	0.94	0.435
Season x Intensity x Time	6	24	0.07	0.999
Sucker height (cm)				
Season	2	4	20.21	0.008
Intensity	3	18	7.23	0.002
Season x Intensity	6	18	2.89	0.038
Time	1	24	43.16	<0.000
Season x Time	2	24	0.04	0.960
Intensity x Time	3	24	9.26	0.000
Season x Intensity x Time	6	24	3.61	0.011
Leader length (cm)				
Season	2	3.86	101.40	0.001
Intensity	3	17.7	8.66	0.001
Season x Intensity	6	17.6	2.54	0.059
Time	1	24.1	165.09	<0.000
Season x Time	2	24.1	6.37	0.006
Intensity x Time	3	24.1	4.41	0.013
Season x Intensity x Time	6	24	3.72	0.009
Current year twigs/ha				
Season	2	4	33.03	0.003
Intensity	3	18	6.77	0.003
Season x Intensity	6	18	1.57	0.213
Time	1	24	166.89	< 0.000
Season x Time	2	24	26.95	<0.000
Intensity x Time	3	24	9.75	0.000
Season x Intensity x Time	6	24	0.90	0.511
Buds/ha				
Season	2	4	26.52	0.005
Intensity	3	18	6.62	0.003
Season x Intensity	6	18	1.62	0.198
Time	1	24	234.41	< 0.000
Season x Time	2	24	41.25	<0.000
Intensity x Time	3	24	10.72	0.000
Season x Intensity x Time	6	24	1.12	0.379
Basal area (m²/ha)				
Season	2	4	2.73	0.179
Intensity	3	18	1.83	0.177
Season x Intensity	6	18	0.57	0.751
Time	1	24	283.66	<0.000
Season x Time	2	24	11.29	0.000
Intensity x Time	3	24	2.61	0.075
Season x Intensity x Time	6	24	0.72	0.641

¹P- value considered significant at $P < 0.05$; ANOVA = analysis of variance; Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

Sucker Height. One year after clipping, sucker height growth for early summer treated suckers appeared to be restricted at any clipping intensity relative to the control (Fig. 4.2B). Early-clipped suckers were still similar to the heights of suckers at the beginning of early summer in 2006 before any clipping treatments had been applied (Figs. 4.2A-B). For example, heights of suckers clipped at 20%, 40%, and 60% intensities were 78 cm, 57 cm, and 67 cm shorter than the control suckers at the beginning of early summer in 2007. Clipping at 20% and 40% intensities in mid-summer, did not affect sucker height relative to the control, but 60% clipping resulted in suckers that were 23 cm shorter than the controls (Fig. 4.2B). Also, clipping in mid-summer, at 20% intensity resulted in suckers that were taller than those clipped at 60% intensity. Similarly, clipping at 20% and 40% intensity in late summer was not detrimental to sucker height compared to the control, but clipping at 60% intensity resulted in suckers that were 40 cm shorter than the control (Fig. 4.2B). Also, 60% clipping in late summer, resulted in suckers that were shorter than those clipped at 20% and 40% intensities. Apart from suckers that were intensely (60%) clipped in mid- and late summer, sucker height increased substantially between the two times (Figs. 4.2A-B). These differences were manifested as a significant season x intensity x time interaction in the ANOVA (Table 4.1).

Leader Length. Clipping treatments affected leader length differently for the different seasons (Fig. 4.3B). One year after clipping, leader length for suckers that were clipped in early summer was not affected by clipping relative to the control. However, the same could not be said for mid- and late summer clipping. Clipping at these seasons resulted in suckers that had substantially more ($P < 0.000$) leader length than the control,

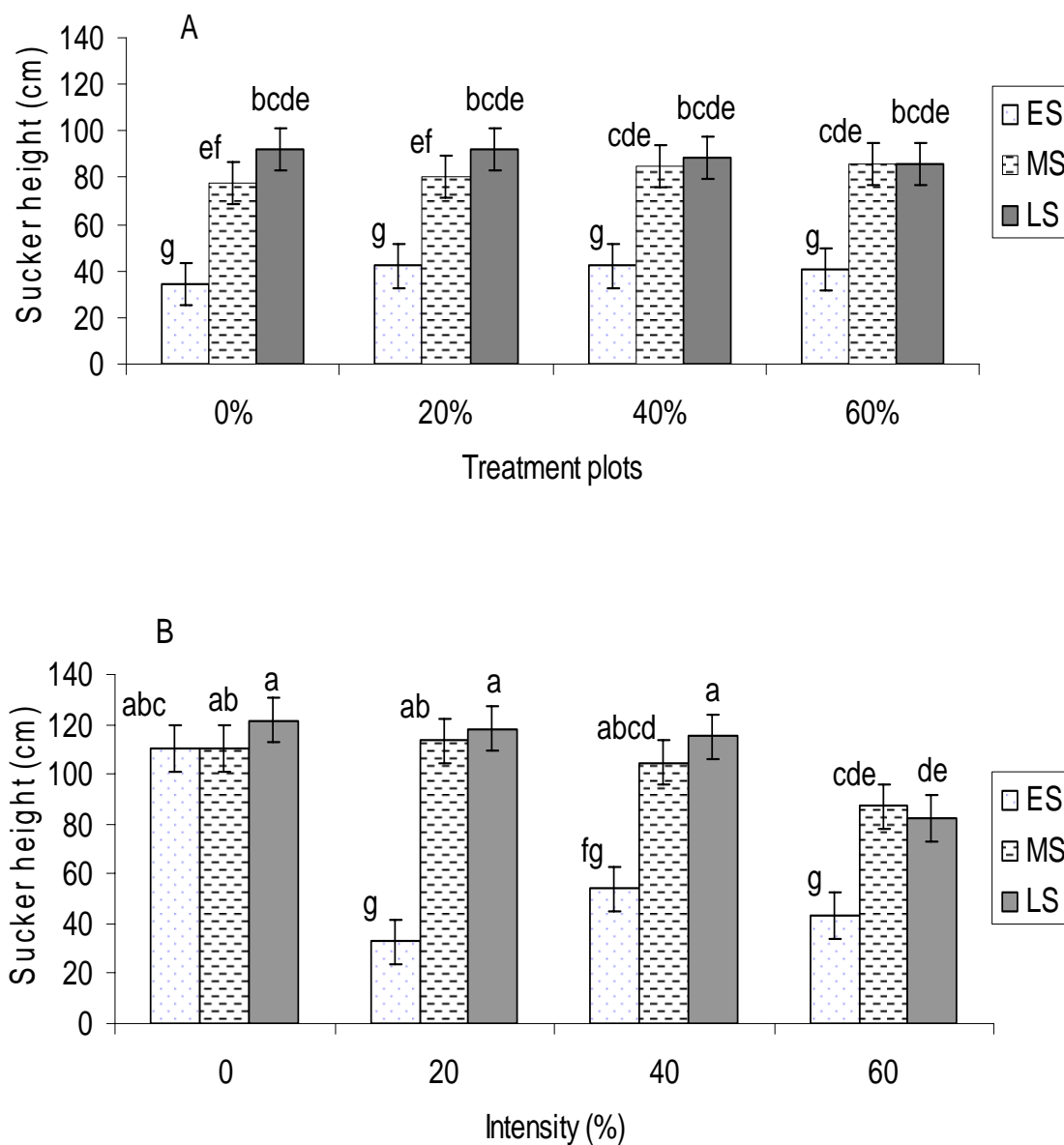


Figure 4.2. Initial mean sucker heights for the treatments plots (A) before clipping in 2006, and (B) effect of season and intensity of clipping on mean sucker height, one year after clipping at the beginning of the growing seasons in 2007. ES = early summer; MS = mid-summer; LS = late summer. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

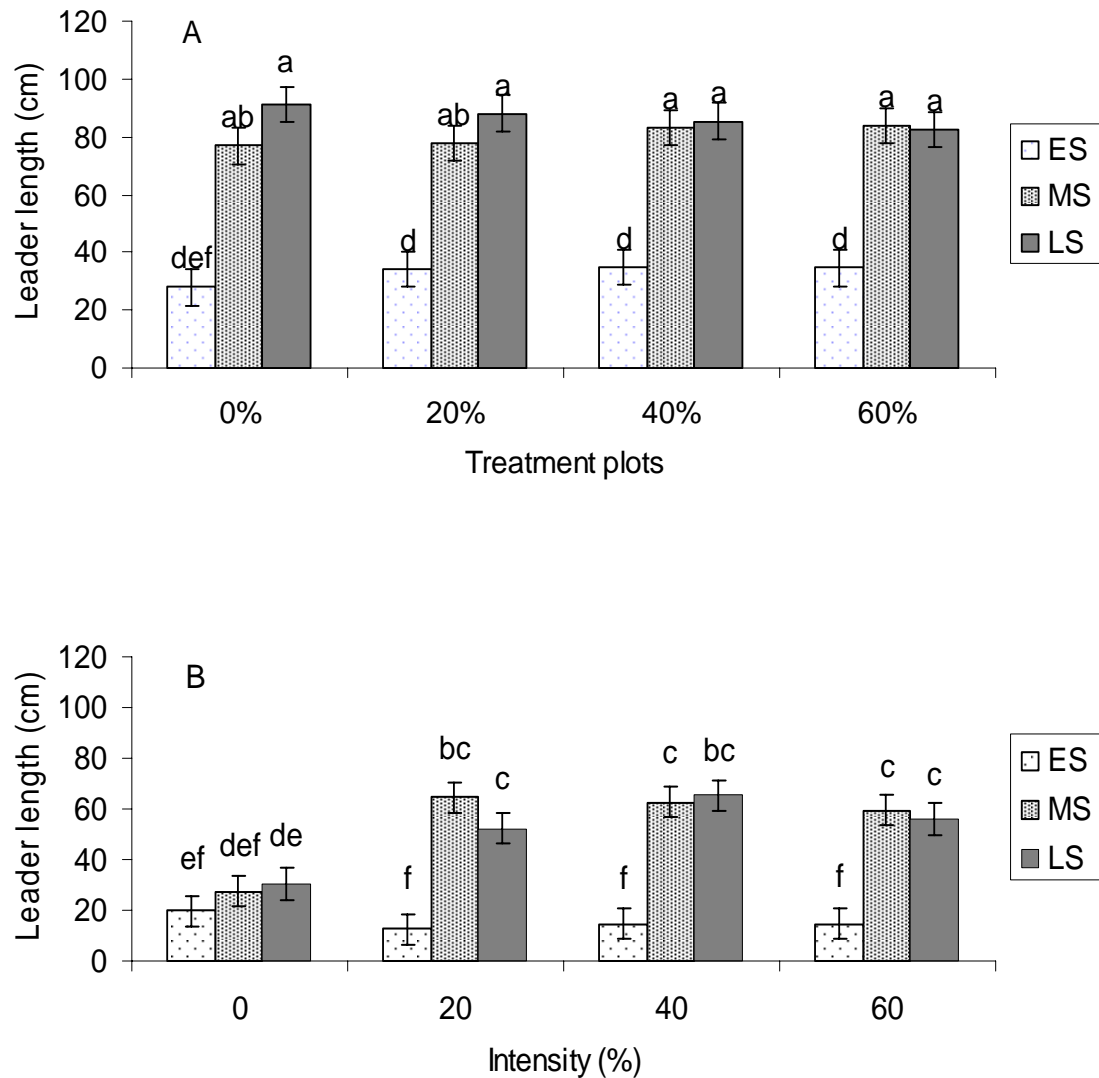


Figure 4.3. Initial mean leader length for the treatment plots (A) before clipping in 2006, and (B) effect of season and intensity of clipping on mean leader length, one year after clipping at the beginning of the growing seasons in 2007. Leader lengths at the beginning of seasons in 2006 closely approximated sucker heights because most suckers emerged during spring and summer that year. ES = early summer; MS = mid-summer; LS = late summer. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

one year after clipping (Fig. 4.3B). However, there was no difference among intensities for any particular season of clipping. Generally, leader length for mid- and late-summer plots was for the most part higher at the beginning of seasons in 2006, than at the same time in 2007 (Figs. 4.3A-B). These results reported a significant season x intensity x time interaction (Table 4.1).

Twig Density. Intensity and time interacted for twig density (Table 4.1).

Overall, twig density increased from time B06 to B07 across all clipping intensities and the control (Fig. 4.4A; see also Fig. E.1A). However, by time B07, all plots that were clipped had fewer ($P \leq 0.047$) twigs/ha than the control. In addition, plots clipped at 20% and 40% intensities had more ($P \leq 0.008$) twigs/ha than those clipped at the 60% intensity (Fig. 4.4A).

Season and time interacted for twig density (Table 4.1), suggesting that twig production was not uniform across seasons (Figs. 4.4B and E.1B). The season when clipping occurred affected twig density. Generally, the number of twigs increased substantially from time B06 to B07 for all seasons, suggesting that the canopies of suckers were expanding. However, clipping in mid- and late summer resulted in far fewer ($P < 0.000$) twigs/ha compared to clipping in early summer (Fig. 4.4B).

Bud Density. Clipping affected bud density (Table 4.1), and indicated that increasing clipping intensity resulted in disproportionately fewer buds/ha compared to the control by time B07 (Fig. 4.5A; see also Fig. E.2A). More ($P \leq 0.046$) buds/ha were present in the control plots compared to the rest of the clipping intensities at time B07. In addition, intense clipping (60%) reduced ($P \leq 0.007$) bud density compared to clipping at 20% and 40% intensities.

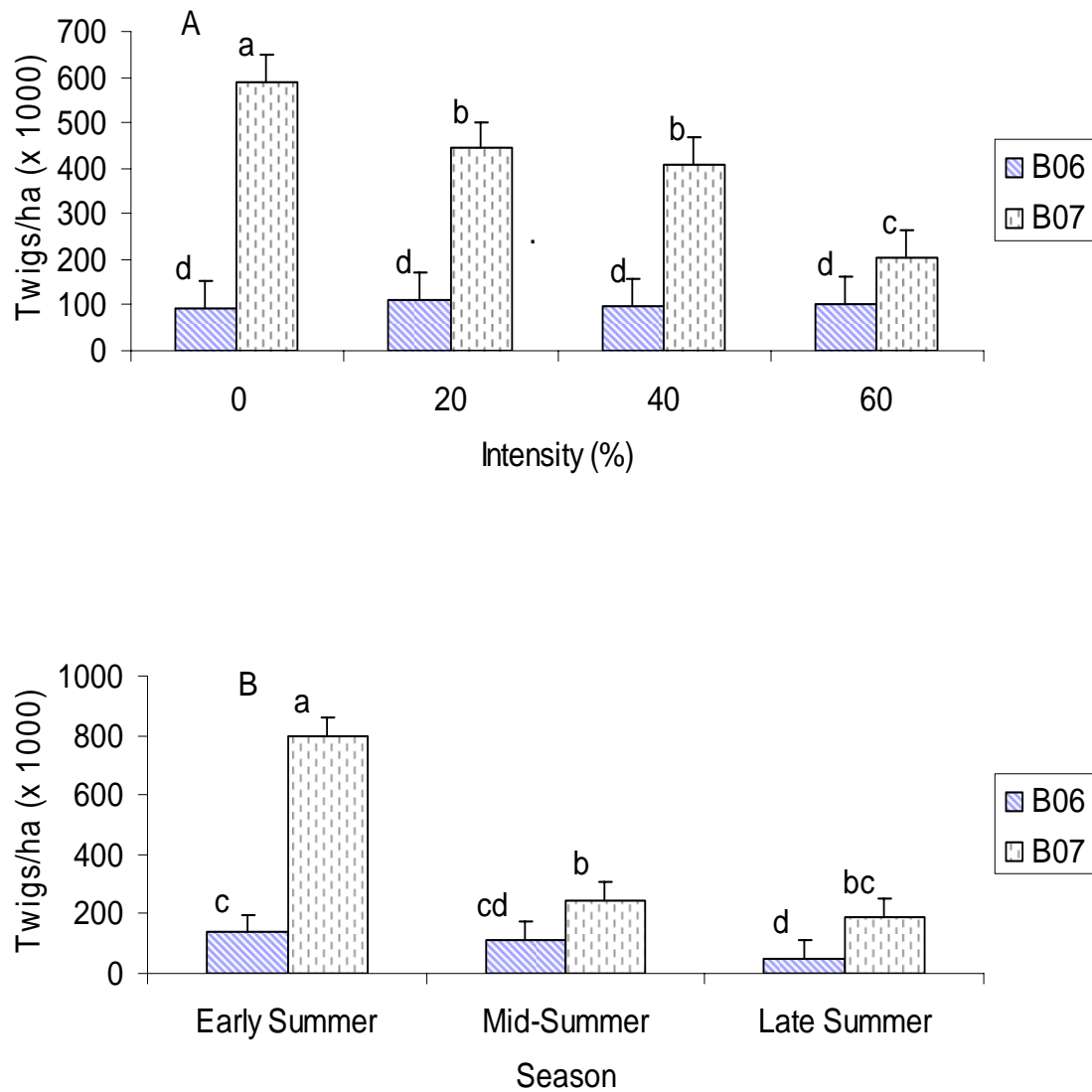


Figure 4.4. Mean comparisons for twig density (A) before clipping in 2006 and 2007, under the different intensities, (B) before clipping in 2006 and 2007, under the different seasons at Cedar Mountain, Utah. B06, B07 = before suckers were clipped at the beginning of seasons in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

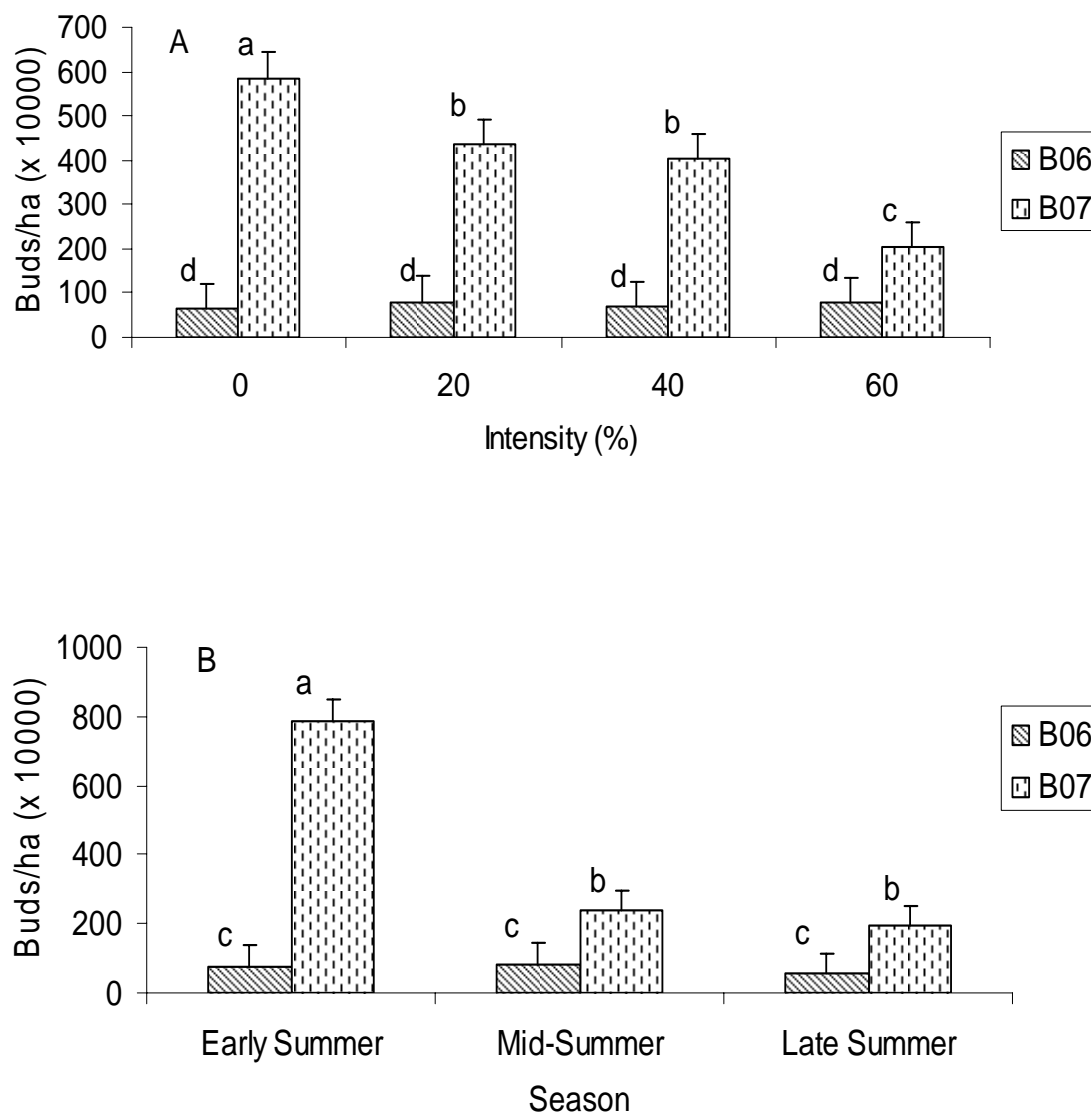


Figure 4.5. Mean comparisons for bud density (A) before clipping in 2006 and 2007, under the different intensities, (B) before clipping in 2006 and 2007, under the different seasons at Cedar Mountain, Utah. B06, B07 = before suckers were clipped at the beginning of seasons in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

Season of clipping and time also interacted for bud density (Table 4.1). The season when clipping occurred, affected bud production (Fig. 4.5B; see also Fig. E.2B). Clearly, bud density increased from time B06 to B07 across seasons. Similar patterns observed for twig density were also evident for bud density. Clipping in mid- and late summer reduced ($P < 0.000$) bud production compared to early summer clipping.

Basal Area. Overall, basal area of suckers increased from time B06 to B07. Basal area growth of suckers was least ($P \leq 0.019$) in early summer compared to mid- and late summer season at time B06 (Fig. 4.6), demonstrating that suckers were continuously growing. Although basal area for early summer plots was less than for the other seasons at time B06, basal area for early summer plots were not statistically different from mid- and late summer plots by time B07. These results showed a significant season and time interaction for basal area growth (Table 4.1). Apparently, intensity of clipping did not significantly affect basal area of suckers.

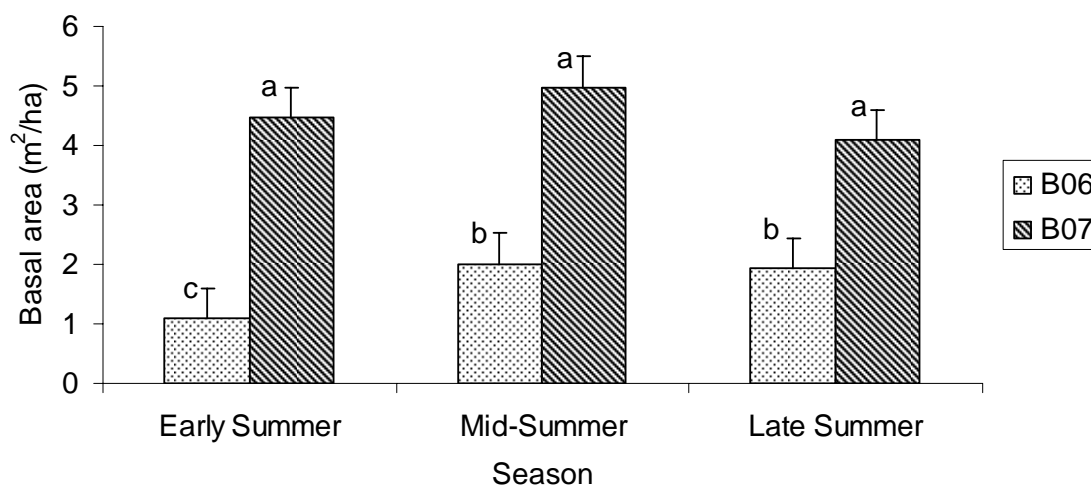


Figure 4.6. Mean comparisons of basal area before clipping in 2006 and 2007, for three seasons. B06, B07 = before suckers were clipped at the beginning of seasons in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

Effects of Intensity and Season of Clipping on Over-Winter Sucker Density Changes

The season when clipping was done certainly affected sucker mortality (Table 4.2; Fig. 4.7). Minimal or no reduction in sucker numbers occurred when clipped in early summer. However, clipping in mid-summer resulted in a 41% death of suckers between time A06 and B07, while clipping in late summer caused a 42% death loss. More suckers died when treatments were applied in mid- and late summer than in early summer. Meanwhile, intensity of clipping did not significantly affect the over-winter dynamics of suckers (Table 4.2).

Effects of Repeated Clipping and Season of Clipping on Sucker Responses

Sucker Density. Generally, sucker density decreased from time A06 to A07 for mid- and late seasons (Table 4.3; Fig. 4.8). This change reflects sucker deaths over-winter (A06 vs. B07) as well as summer mortality in 2007 (B07 to A07). Clipping in

Table 4.2. ANOVA fixed effects of season, intensity, and time of clipping on sucker density for A06 and B07 comparisons. A06, B07 = the end of the growing season in 2006 and beginning of the growing seasons in 2007, respectively.

Source	Num DF	Den DF	F Value	¹ <i>P - value</i>
Season	2	4	3.10	0.154
Intensity	3	18	1.65	0.212
Season x Intensity	6	18	1.40	0.268
Time	1	24	25.77	< 0.000
Season x Time	2	24	12.12	0.000
Intensity x Time	3	24	0.79	0.512
Season x Intensity x Time	6	24	1.23	0.326

¹*P* -value considered significant at $P < 0.05$; ANOVA = analysis of variance; Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

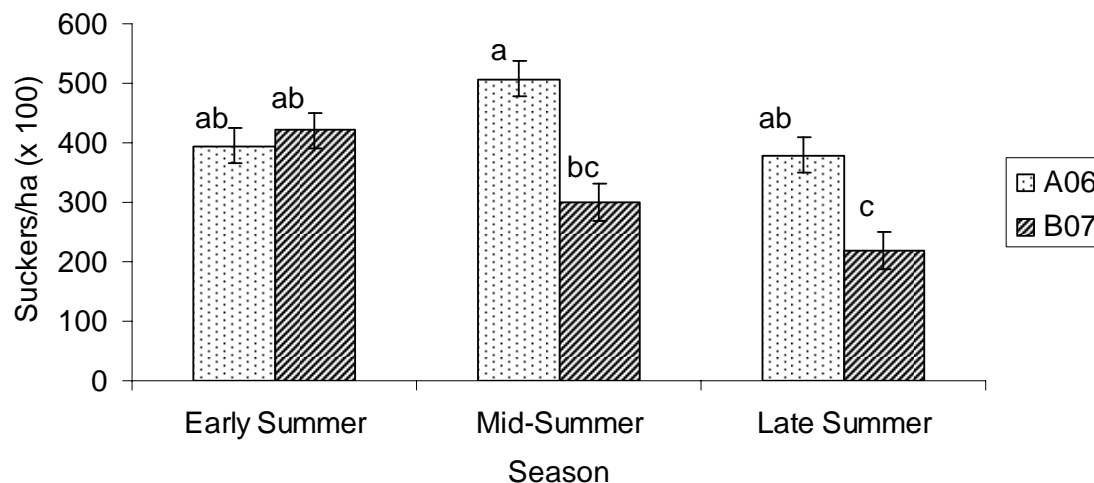


Figure 4.7. Effect of season of clipping on mean sucker density at the end of the growing season in 2006 (A06) and before clipping in 2007 (B07). Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

mid- and late summer caused a 48% and 46% reduction in sucker numbers, respectively, compared to 12% observed when they were clipped in early summer. However, it is interesting to note that early summer clipped plots endured the same conditions as those for the other two seasons, but fewer suckers were lost in that treatment. As noted above, intensity of clipping did not affect the dynamics of suckers differently between the two times (Table 4.3). Meanwhile, a minimal and inconsequential number of new suckers that could influence the dynamics of sucker densities were noted in the summer of 2007 (Fig. E.3).

Sucker Height. Generally, sucker height decreased as the intensity of clipping increased (Table 4.3; Fig. 4.9) as might be expected. On average, clipping at 20%, 40%, and 60% intensities caused a 40, 48, and 65 cm reduction in height, respectively, compared to the control.

Table 4.3. ANOVA fixed effects of season, intensity, and time of clipping on sucker density, sucker height, leader length, current year twigs, bud density, and basal area growth for A06 (the end of the growing season in 2006) and A07 (the end of the growing season in 2007) data.

Source	Num DF	Den DF	F- Value	¹ P- value
Suckers/ha				
Season	2	4	4.65	0.090
Intensity	3	18	2.05	0.143
Season x Intensity	6	18	1.86	0.143
Time	1	24	37.07	< 0.000
Season x Time	2	24	5.99	0.008
Intensity x Time	3	24	0.76	0.528
Season x Intensity x Time	6	24	0.66	0.681
Sucker height (cm)				
Season	2	3.92	0.10	0.907
Intensity	3	17.1	57.84	< 0.000
Season x Intensity	6	16.9	2.15	0.101
Time	1	20.7	137.04	< 0.000
Season x Time	2	20.5	1.07	0.362
Intensity x Time	3	20.5	0.35	0.790
Season x Intensity x Time	6	20.2	1.74	0.164
Leader length (cm)				
Season	2	3.74	2.30	0.224
Intensity	3	17	68.56	< 0.000
Season x Intensity	6	16.6	4.37	0.008
Time	1	21	95.34	< 0.000
Season x Time	2	20.7	2.36	0.119
Intensity x Time	3	20.7	44.09	< 0.000
Season x Intensity x Time	6	20.4	1.23	0.334
Current year twigs/ha				
Season	2	4	4.85	0.085
Intensity	3	18	7.24	0.002
Season x Intensity	6	18	0.41	0.865
Time	1	24	284.10	< 0.000
Season x Time	2	24	10.51	0.001
Intensity x Time	3	24	12.29	< 0.000
Season x Intensity x Time	6	24	0.13	0.992
Buds/ha				
Season	2	4	3.61	0.127
Intensity	3	18	18.50	< 0.000
Season x Intensity	6	18	0.53	0.780
Time	1	24	196.57	< 0.000
Season x Time	2	24	13.54	0.000
Intensity x Time	3	24	3.84	0.022
Season x Intensity x Time	6	24	0.22	0.966
Basal area (m²/ha)				
Season	2	4	1.50	0.326
Intensity	3	18	1.86	0.172
Season x Intensity	6	18	1.37	0.279
Time	1	24	55.43	< 0.000
Season x Time	2	24	6.15	0.007
Intensity x Time	3	24	0.71	0.557
Season x Intensity x Time	6	24	0.87	0.529

¹P -value considered significant at $P < 0.05$; ANOVA = analysis of variance; Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

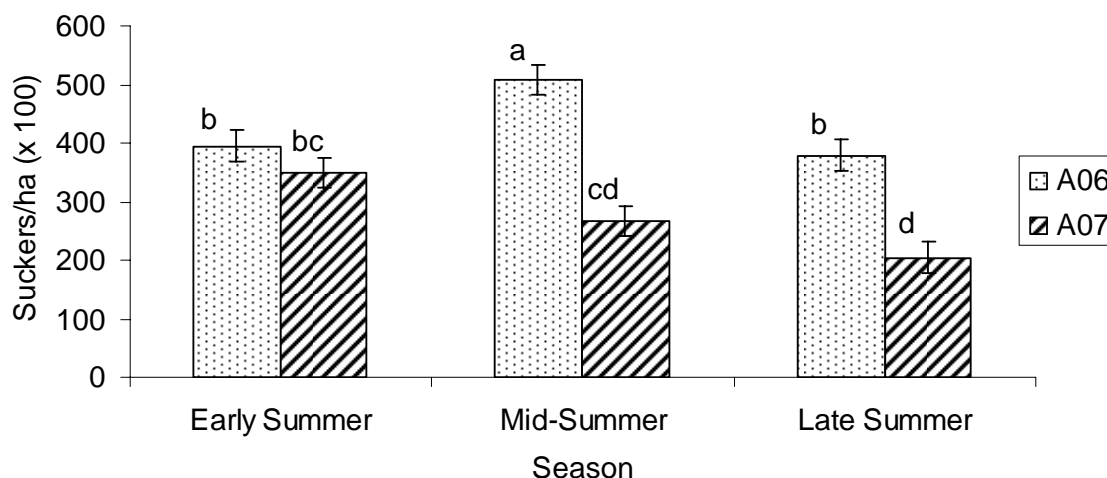


Figure 4.8. Effect of season of clipping on mean sucker density at the end of the growing season in 2006 (A06) and 2007 (A07), respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

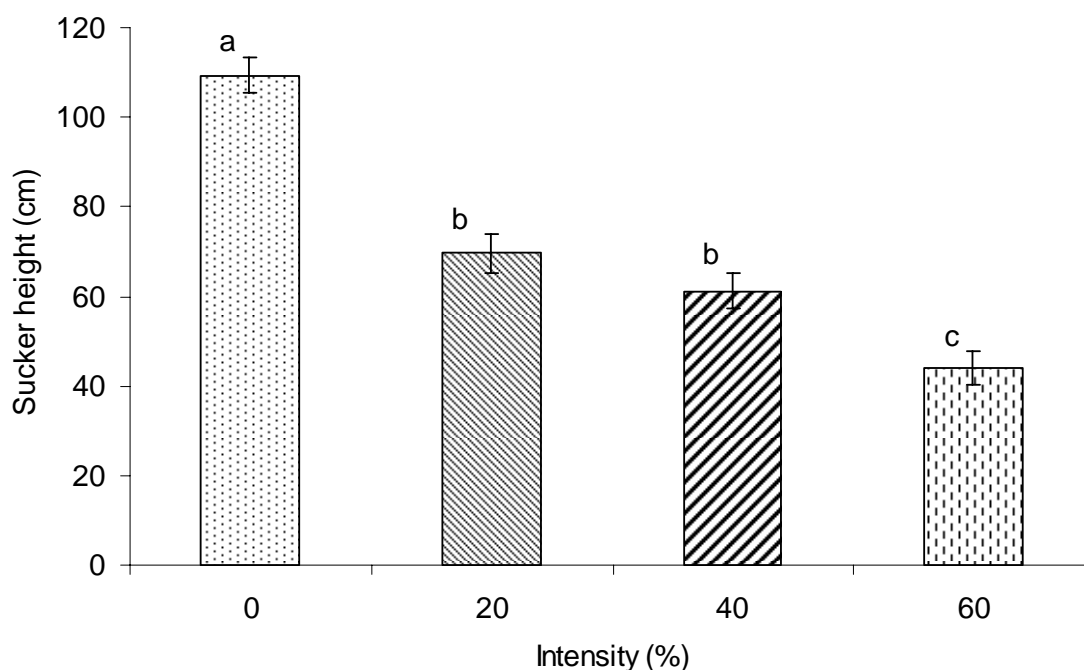


Figure 4.9. Effect of clipping intensity on mean sucker height averaged over times A06 and A07. A06, A07 = the end of the growing season in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

Leader Length. Intensity of clipping and time interacted for leader length (Table 4.3). Generally, leader length was reduced by clipping at time A06, but not at time A07, compared to the control (Fig. 4.10; see also Fig. E.4). With the exception of suckers clipped at 20% intensity, leader length was not different for plots clipped at 40% and 60% intensities between the two times (Fig. 4.10). Interestingly, except for intense (60%) clipping, leader length of clipped suckers was not affected by clipping compared to the control by time A07.

Twig Density. Intensity and time interacted for twig density (Table 4.3). Overall, the effects of clipping on twig numbers were more pronounced at time A07, than at A06 (Fig. 4.11A; see also Fig. E.5). By time A07, twig densities were reduced ($P \leq 0.013$) by 32%, 54%, and 70% by clipping at 20%, 40%, and 60% intensities, respectively, compared to the control (Fig. 4.11A).

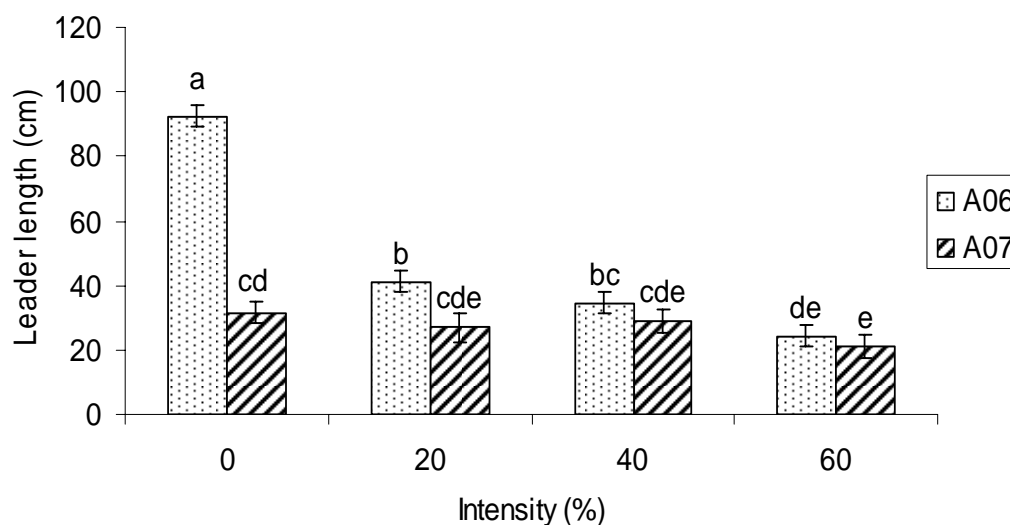


Figure 4.10. Effect of clipping intensity on mean leader length. A06, A07 = the end of the growing season in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

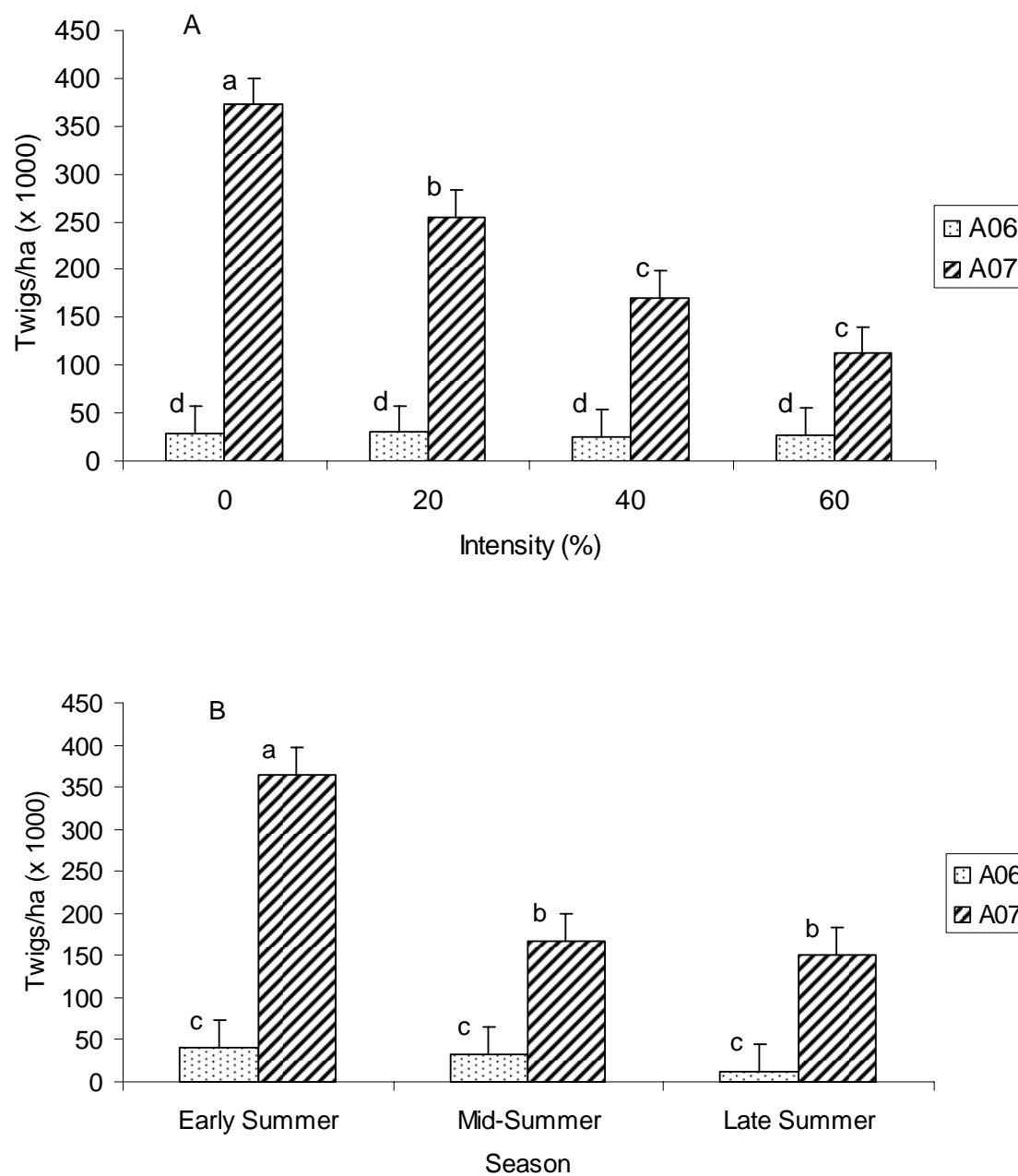


Figure 4.11. Effect of clipping intensity (A) and season of clipping (B) on mean twig density at the end of the growing season in 2006 (A06) and 2007(A07), respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

By A07, advancing season of clipping clearly reduced twig density (Fig. 4.11B). Mid- and late summer clipping were more detrimental to twig production than early summer clipping. By time A07, about 55% and 59% fewer twigs were present in plots clipped in mid- and late summer, respectively, compared to early summer. The results represented a significant season and time interaction in the ANOVA (Table 4.3).

Bud Density. Intensity and time interacted for bud density (Table 4.3). This suggested that increasing clipping intensity led to a proportionately larger reduction in buds/ha compared to the control (Fig. 4.12A; see also Fig. E.6). Fewer ($P \leq 0.009$) buds/ha were present in plots clipped at 40% and 60% intensity than in control plots, at time A06 (Fig. 4.12A). By time A07, the effects of clipping, were magnified, compared to the control plots, with about 32%, 56%, and 70% fewer buds being present on the 20%, 40%, and 60% clipped plots, respectively (Fig. 4.12A).

Bud production was also affected by season of clipping (Table 4.3; Fig. 4.12B). Clipping in early summer was least ($P \leq 0.009$) detrimental to bud production compared to clipping in mid- and late summer by time A07 (Fig. 4.12B). Overall, bud density increased substantially between A06 and A07 for all seasons of clipping (593%, 243%, and 314% for early, mid-, and late summer treatments, respectively).

Basal Area. Basal area of suckers was not affected by season of clipping at time A06, but season of clipping affected basal area at time A07 (Fig. 4.13). Clipping in late summer limited basal area growth of suckers compared to clipping in early summer by time A07. Notably, clipping in early summer resulted in a 172% increase in basal area, while clipping in mid- and late summer resulted in an increase of around 60-70% in basal area, between the two times. The trend established here, followed that observed for

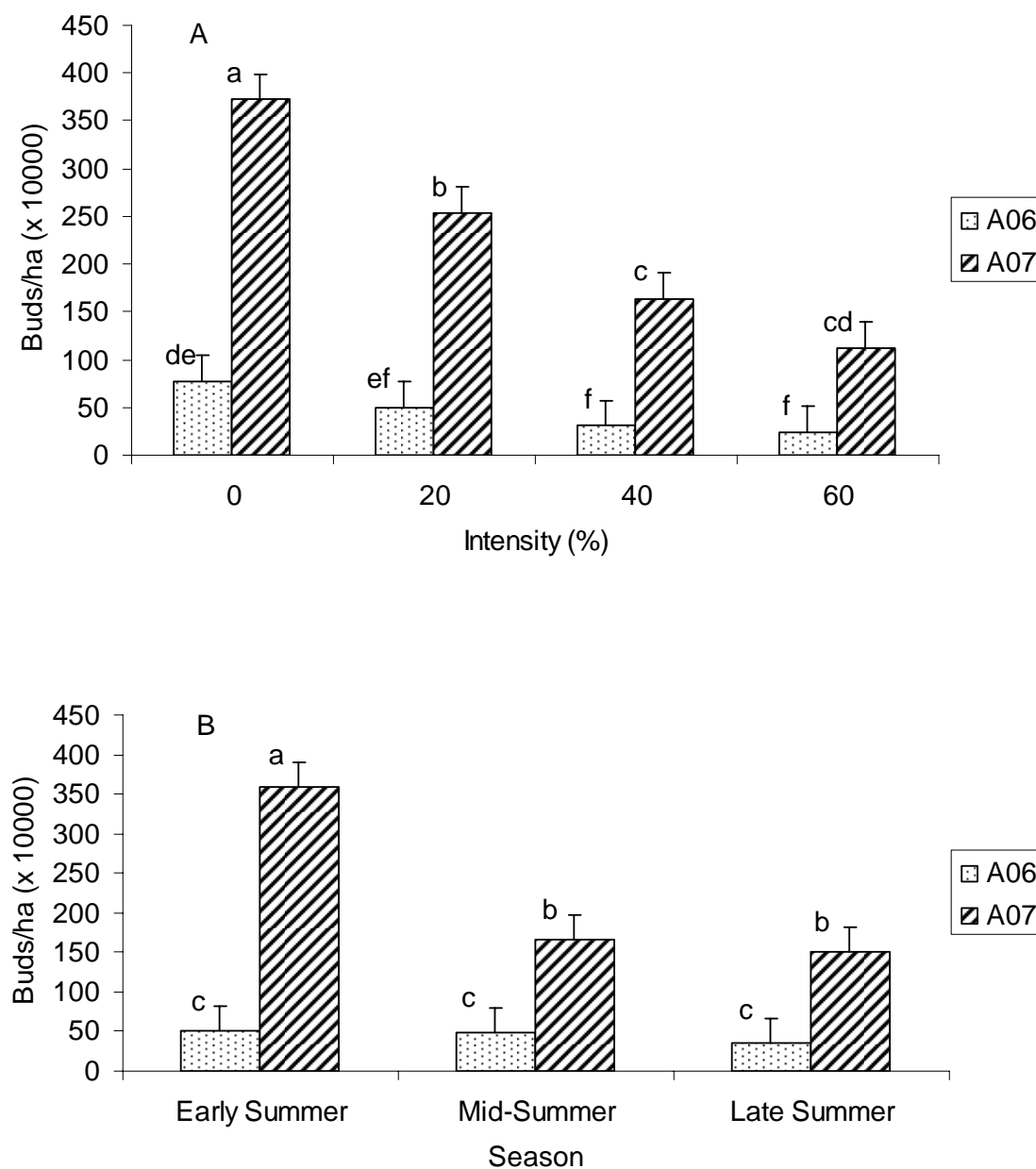


Figure 4.12. Effect of clipping intensity (A) and season of clipping (B) on mean bud density at the end of the growing season in 2006 (A06) and 2007 (A07), respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

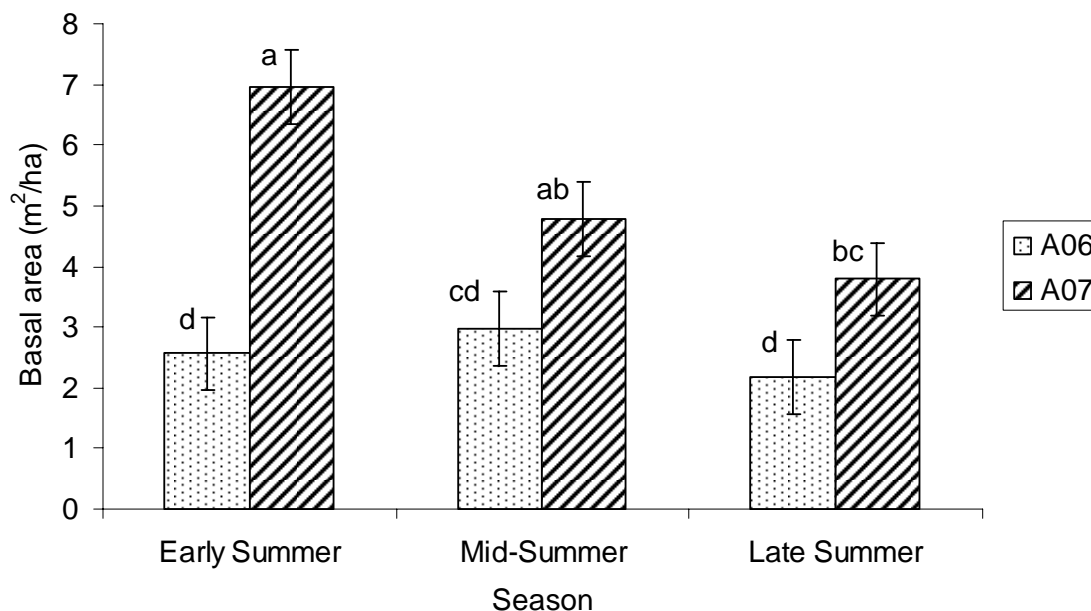


Figure 4.13. Effect of season of clipping on mean basal area at the end of the growing season in 2006 (A06) and 2007 (A07), respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

sucker density. These results reported, showed a season and time interaction for basal area growth (Table 4.3). On the other hand, clipping intensities did not significantly affect basal area growth (Table 4.3).

Differences Between 2006 and 2007 Sucker Responses

Sucker Density. Intensity and year interacted for change in sucker density (Table 4.4). The effects of clipping were more pronounced in 2006 compared to 2007 (Fig. 4.14A; see also Fig. E.7A). Clipping at any intensity reduced the number of suckers in 2006, compared to the control, but even the control saw a small (approximately 5,000 suckers/ha) loss. Interestingly, fewer suckers died in 2007 regardless of clipping intensities. The control did not differ between the years. Suckers coped much better

Table 4.4. ANOVA fixed effects of season, intensity of clipping, and year on the change in sucker density, sucker height, leader length, and basal area growth in 2006 and 2007.

Source	Num DF	Den DF	F- Value	¹ P-value
Suckers/ha				
Season	2	4	19.48	0.009
Intensity	3	18	4.47	0.016
Season x Intensity	6	18	2.36	0.074
Year	1	24	34.32	<0.000
Season x Year	2	24	16.81	<0.000
Intensity x Year	3	24	2.91	0.055
Season x Intensity x Year	6	24	1.32	0.288
Sucker height (cm)				
Season	2	3.97	48.45	0.002
Intensity	3	16.2	56.09	<0.000
Season x Intensity	6	16	1.49	0.246
Year	1	21	0.69	0.415
Season x Year	2	21	22.80	<0.000
Intensity x Year	3	21	19.67	<0.000
Season x Intensity x Year	6	21	1.35	0.280
Leader length (cm)				
Season	2	4.41	148.50	<0.000
Intensity	3	17.2	60.86	<0.000
Season x Intensity	6	16.9	2.05	0.115
Year	1	21	0.22	0.644
Season x Year	2	21	33.48	<0.000
Intensity x Year	3	21	24.76	<0.000
Season x Intensity x Year	6	21	2.36	0.067
Basal area (m²/ha)				
Season	2	4	3.55	0.130
Intensity	3	18	8.52	0.001
Season x Intensity	6	18	5.02	0.004
Year	1	24	11.11	0.003
Season x Year	2	24	0.83	0.448
Intensity x Year	3	24	3.13	0.045
Season x Intensity x Year	6	24	1.37	0.268

¹P- value considered significant at $P < 0.05$.

ANOVA = analysis of variance.

Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

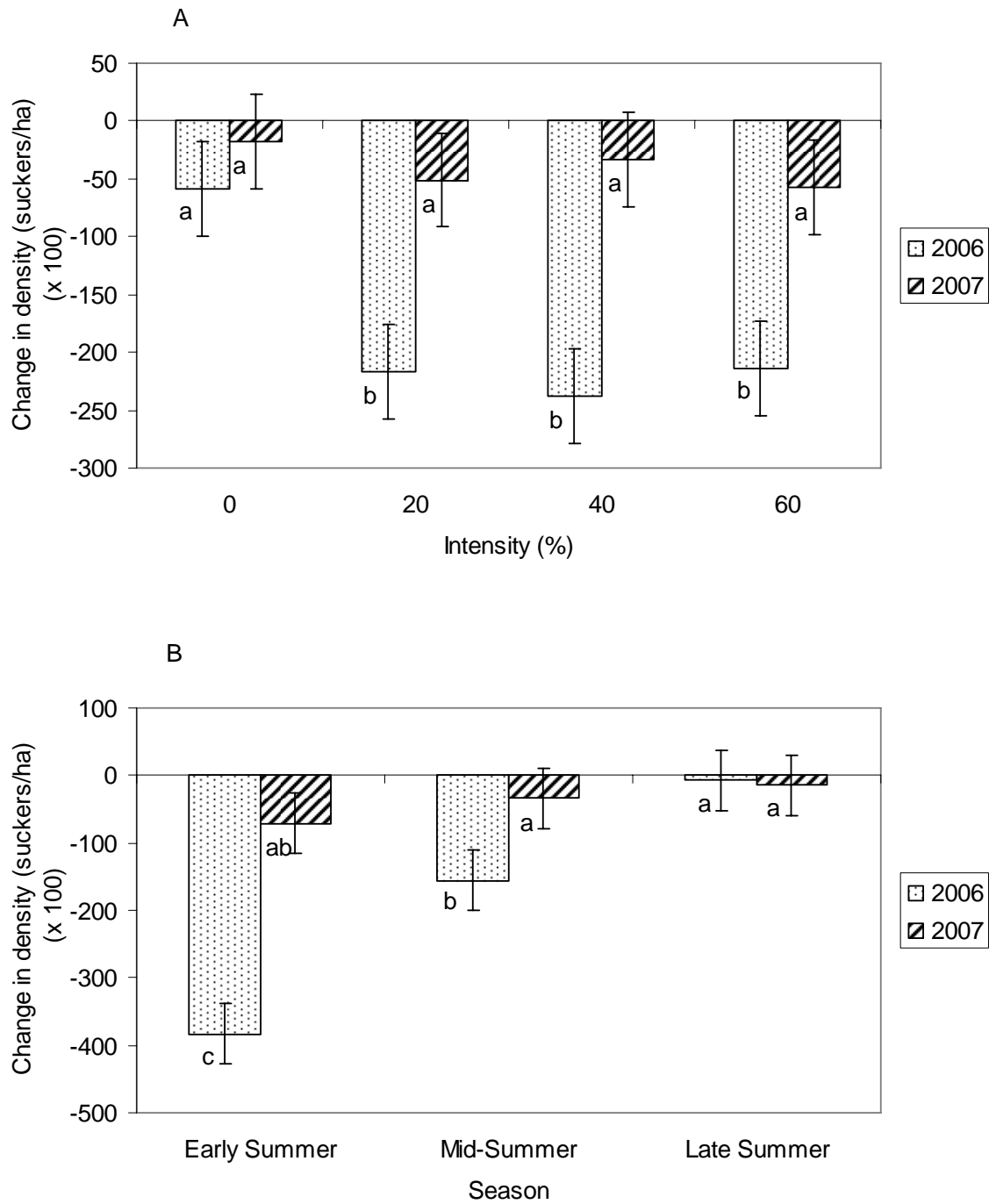


Figure 4.14. The effect of clipping intensity (A), and season of clipping (B) on mean sucker density changes for 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

with the effects of clipping in 2007, probably because the suckers then were more mature and the weak ones had been eliminated in their first year of life.

Season of clipping affected sucker survival, also (Table 4.4). More ($P \leq 0.001$) suckers were lost especially when clipped in early summer than in mid- or late summer, and particularly so in 2006 (Fig. 4.14B; see also Fig. E.7B). Also, the results indicate that clipping in mid- summer was more harmful ($P = 0.029$) to sucker survival compared to clipping in late summer in the first year. These trends are obviously due to phenological differences when clipping treatments were applied. Late summer clipping came later in the growing season, and as expected, fewer suckers would likely die before the end of the current growing season. In 2007, sucker mortality was not different regardless of season and far fewer suckers died compared to 2006, especially considering early- and mid-summer treatments.

Sucker Height. Clipping reduced ($P \leq 0.000$) sucker height growth in both years, compared to the control, and sucker height growth was affected more as the intensity of clipping increased, especially in 2006 (Fig. 4.15A; see also Fig. E.8A). Interestingly, the control suckers did not grow as much in 2007, as in 2006 (7 vs. 28 cm, respectively; Fig. 4.15A). The results reported showed a significant intensity and year interaction for sucker height (Table 4.4).

Season of clipping and year interacted for change in sucker height (Table 4.4). On average, clipping in early summer resulted in an increase in sucker height in both years (especially in 2006) (Fig. 4.15B; see also Fig. E.8B), suggesting suckers had time to re-grow before the current season was over. Conversely, clipping in mid- and late summer caused a reduction in sucker height in both years. Clipping in mid- and late

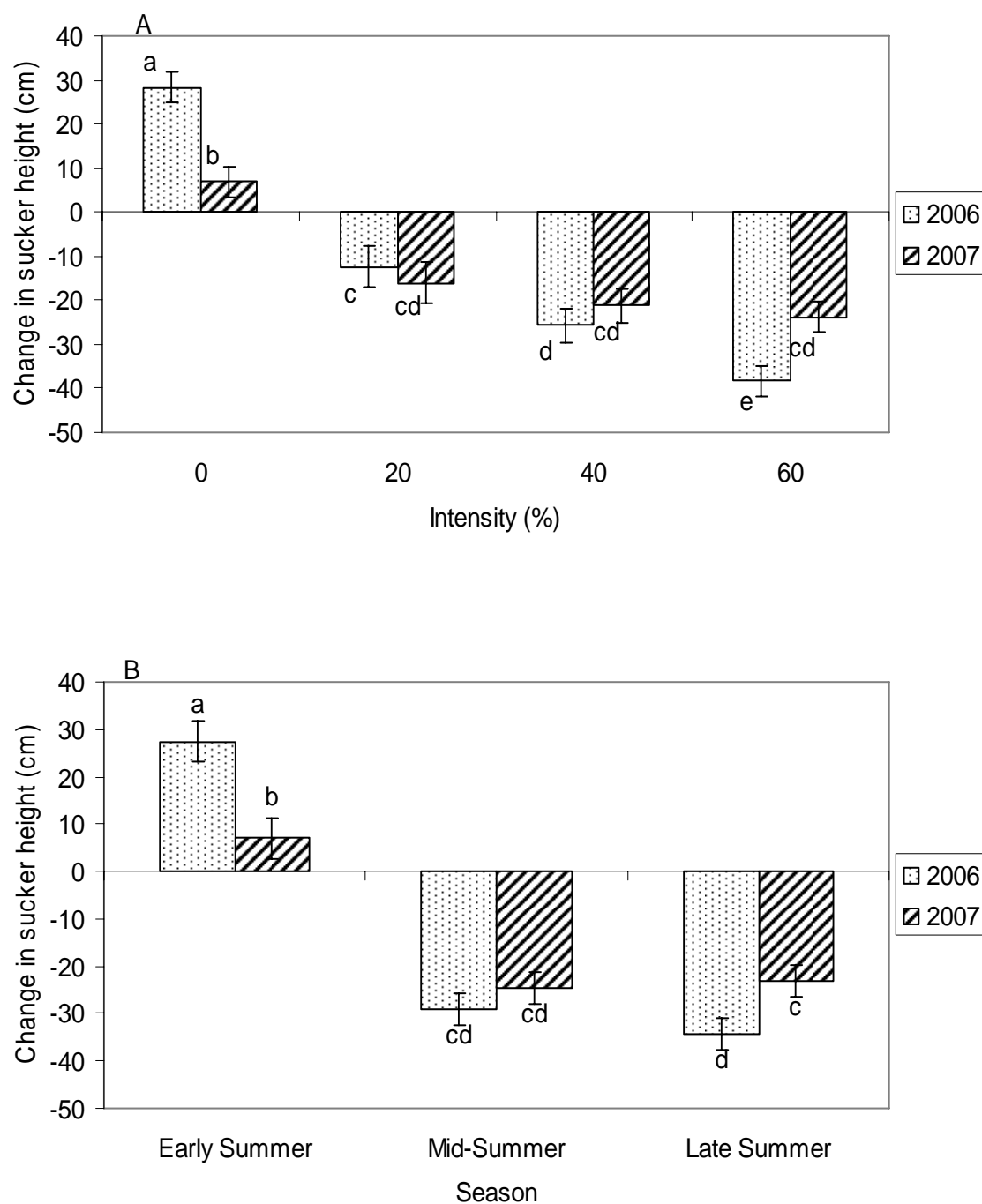


Figure 4.15. The effect of intensity (A), and season (B) of clipping on mean sucker height changes for 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

summer simply did not allow suckers enough time to re-grow and re-gain their pre-clipping status before the end of growing season.

Leader Length. Intensity and year interacted for change in leader length (Table 4.4), suggesting that clipping affected leader length differently between the years. Clearly, clipping affected leader length in both years, compared to the control, and leader length tended to decrease more as the intensity of clipping increased (Fig. 4.16A; see also Fig. E.9A). This is a similar pattern seen above in the case of change in height growth (Fig. 4.15A). On average, control suckers gained 28 cm and 5 cm in 2006 and 2007, respectively.

Leader length was affected differently by the season of clipping (Table 4.4; Fig. 4.16B; see also Fig. E.9B). Clipping in early summer resulted in a positive gain in leader length, compared to mid- and late summer clipping, and 2006 showed the greatest gain (27 cm), compared to 2007 (7 cm) (Fig. 4.16B). Suckers clipped in mid- and late summer did not lose as much leader length in 2007, as in 2006 (Fig. 4.16B), suggesting that suckers coped much better with clipping as they grew bigger.

Basal Area. Intensity and year interacted for change in basal area (Table 4.4; Fig. 4.17). Clipping affected basal area growth in 2006, compared to the control. However, in 2007, clipping did not statistically affect basal area growth differently from the control, though there was a tendency for the control suckers to be numerically higher than for the clipping intensities. Meanwhile, season of clipping did not significantly affect change in basal area. Averaged across the three seasons, basal area growth was approximately $0.8 \pm 0.3 \text{ m}^2/\text{ha}$ and $0.4 \pm 0.3 \text{ m}^2/\text{ha}$ in 2006, and 2007, respectively.

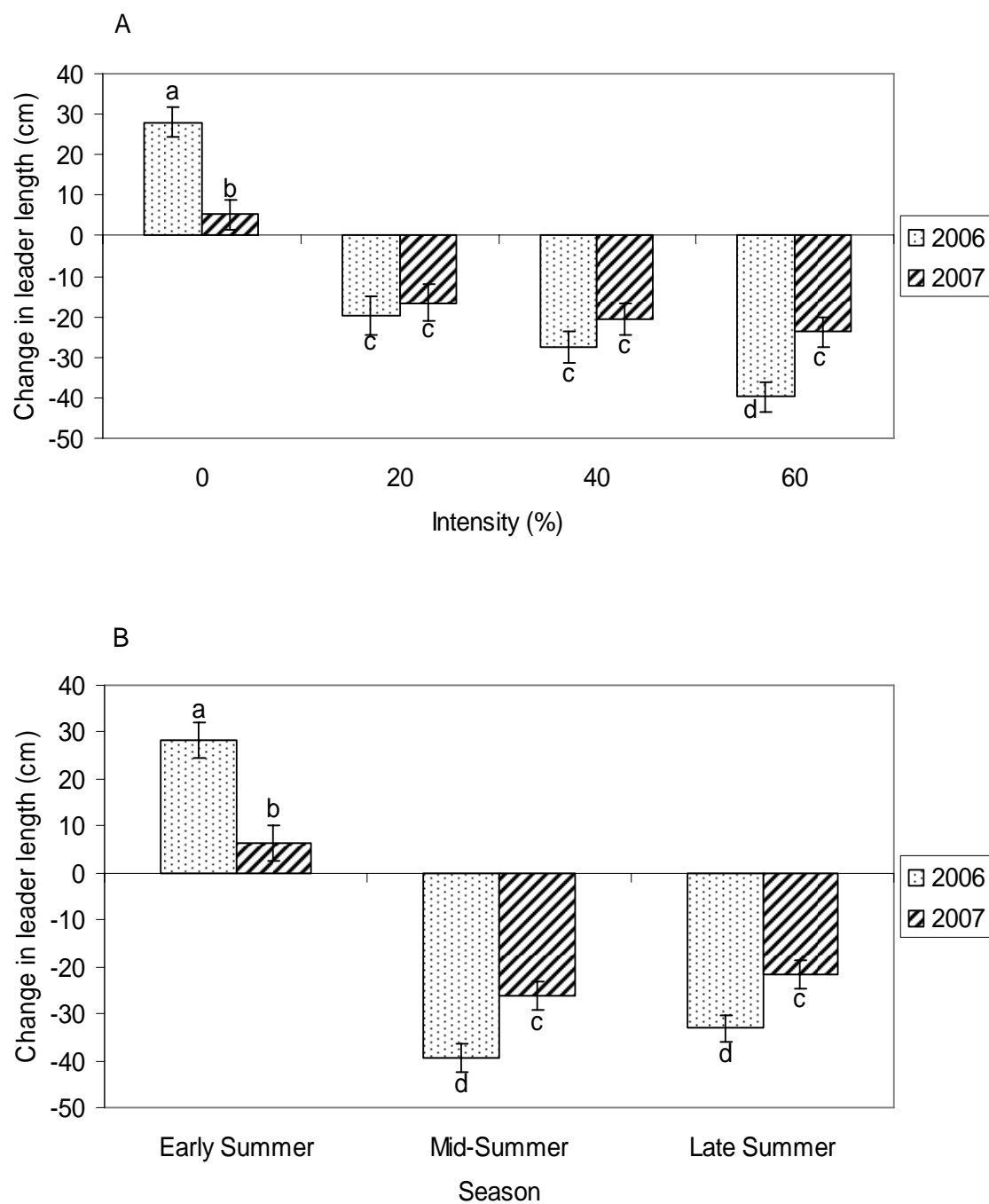


Figure 4.16. The effect of intensity (A), and season (B) of clipping on mean leader length changes for 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

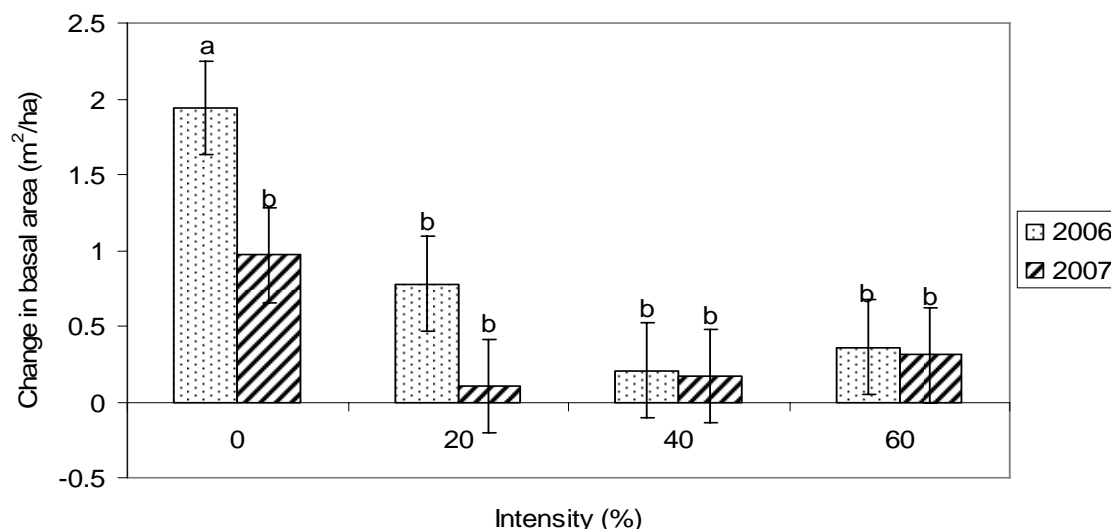


Figure 4.17. The effect of clipping intensity on mean basal area changes for 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

Windows of Mortality

Clearly, clipping in early summer in the first year of growth resulted in more suckers dying compared to clipping in mid- or late summer (Figs. E.10A-C). Natural mortality of suckers on the control plots was about 16% between the beginning and the end of the growing season in 2006. In contrast, plots clipped in early summer saw an approximately 60-64% mortality of suckers between these times (Fig. E.10A). Meanwhile, clipping in mid- and late summer resulted in approximately 11-23% and 6-14% mortality, respectively, between the beginning of the treatments and the end of the growing season in the first year (Figs. E.10B-C).

Minimal mortality was noted in early summer treated plots over-winter (October-June time period) (Fig. E.10A). However, for plots that were treated in mid- and late

summer, mortality ranged from 42-54% and 36-46%, respectively, between the end of the growing season in 2006 and beginning of seasons in 2007 (Figs. E.10B-C).

Clipping in the second year of growth resulted in about 6-10%, 2-5%, and 1-6% mortality of suckers, respectively, for early, mid- and late summer treated plots between the beginning of seasons and the end of the growing season (Figs. E.10A-C). In contrast, the control plots saw sucker mortality of about 3%, 1% and 0.2%, respectively, between the beginning of early, mid-, late summer and end of the growing season in 2007.

Plant Nutritional Responses

Crude Protein Content (%). Generally, mean crude protein (%) content decreased with advancing season and intensity of clipping in 2006 (Fig. 4.18A). Unexpectedly, mean crude protein content of aspen leaves (as opposed to leaves and stems for clipped plots) was 7.4%, 5.5%, and 2.6% lower ($P \leq 0.017$) than for suckers clipped at 20%, 40%, and 60% intensities, respectively, in early summer. Mean crude protein content for clipped material at 20% and 40% intensities, was also higher ($P \leq 0.009$) than for material clipped at 60% intensity, for this season. Clipping suckers at 60% intensity, in mid- summer, resulted in material that had a 2.5% lower ($P \leq 0.020$) mean crude protein content compared to the leaves. Material clipped at 20%, 40%, and 60% intensities in late summer, had a 3.1%, 4.1%, and 4.6% lower ($P \leq 0.006$) mean crude protein content, respectively, than the leaves.

Similarly, as in 2006, mean crude protein content of clipped material generally decreased as the growing season advanced in 2007 (Fig. 4.18B). No differences were noted between the leaves and the clipped plots within each season in 2007. However, in

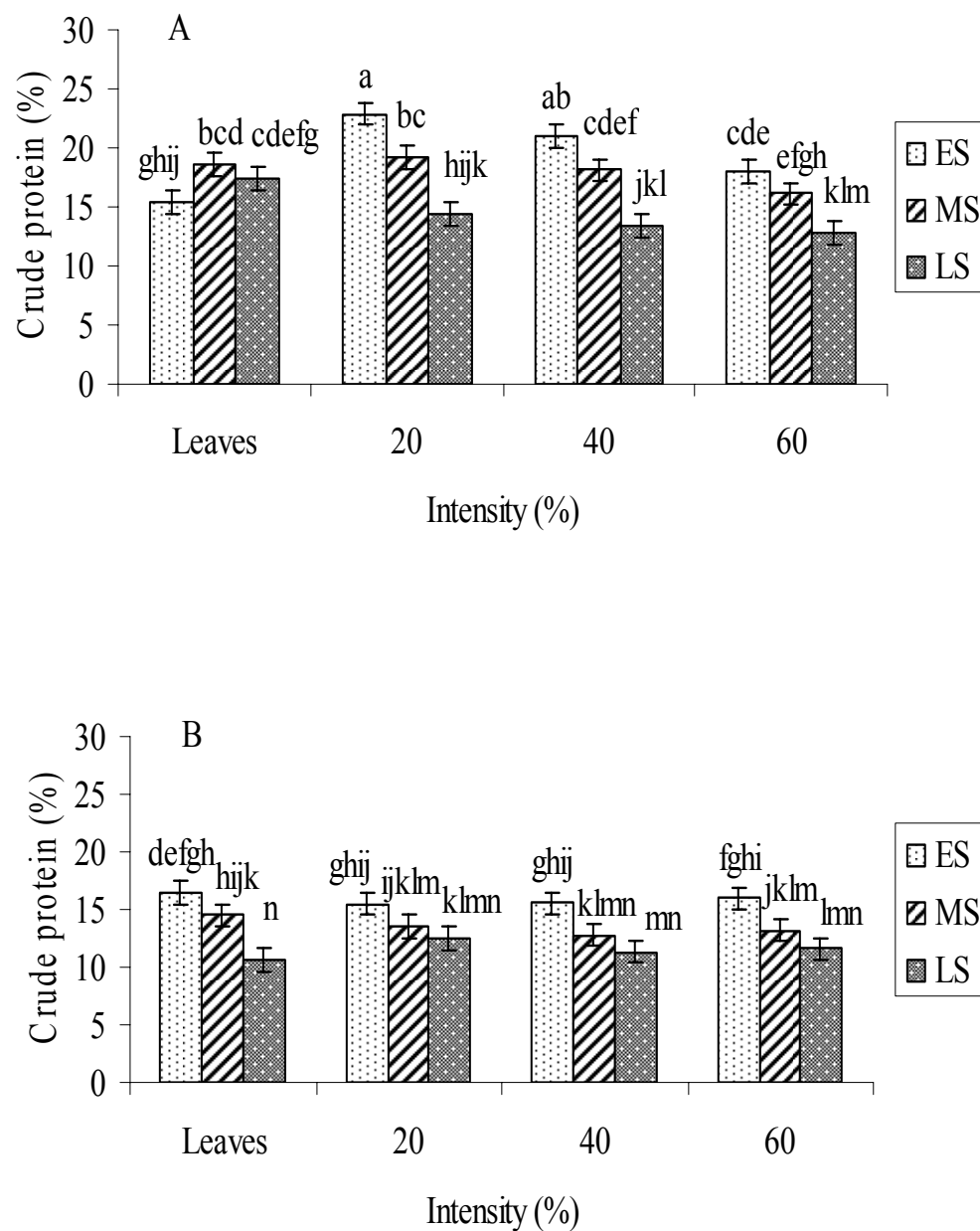


Figure 4.18. Mean crude protein (%) content of aspen leaves and aspen suckers clipped at different intensities and seasons in 2006 (A) and 2007 (B). ES = early summer; MS = mid- summer; LS = late summer. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

2007, crude protein content of material clipped at 20%, 40%, and 60% intensities in early summer were 7.4%, 5.4%, and 2.1% lower, respectively, than in 2006 (Fig. 4.18B). A similar pattern emerged for mid-summer clipping. Crude protein content of material clipped at 20%, 40%, and 60% intensities, and for the leaves were 4.1%, 5.7%, 5.3%, and 2.9% lower, respectively, in 2007 than in 2006. Clipping at 20% and 60% in late summer did not affect crude protein content of material differently between the years, though crude protein levels tended to be numerically lower in 2007, compared to 2006 (Figs. 4.18A-B). However, values for the leaves, and for suckers clipped at 40% intensity in late summer were 6.8% and 2.1% lower in 2007, than in 2006. These results reflect the significant intensity x season x year interaction in the ANOVA (Table 4.5).

In Vitro True Digestibility (%). Generally, IVTD of forages tended to decrease as the intensity of clipping increased and as the growing season progressed, though not by very much. Unexpectedly, material clipped at 20%, and 40% intensities in early summer had higher ($P \leq 0.031$) IVTD than the leaves (Fig. 4.19A). There appeared to be

Table 4.5. ANOVA fixed effects of season and intensity of clipping, and year on mean crude protein content (%) of aspen suckers.

Source	Num DF	Den DF	F Value	¹ P-value
Season	2	4	21.52	0.007
Intensity	3	18	4.35	0.018
Season x Intensity	6	18	3.12	0.028
Year	1	24	184.32	<0.000
Season x Year	2	24	2.85	0.078
Intensity x Year	3	24	5.42	0.005
Season x Intensity x Year	6	24	9.95	< 0.000

¹P -value considered significant at $P < 0.05$; ANOVA = analysis of variance; Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

no apparent reason to substantiate this observation except to attribute it to the fact that the leaves were picked all over the entire plant. As such a decrease in digestibility may be attributed to aging of leaves becoming increasingly less-digestible as they aged. But this seemed unlikely because the growing season had just begun. However, one expects digestibility to decrease with increasing intensity of clipping because of the increase in fiber component (in stems) of harvested material. Not surprising though, plant material clipped at 60% in early summer resulted in a 2.7%, and 2.8% lower ($P \leq 0.022$) IVTD than that clipped at 20% and 40%, respectively. Clipping suckers at 20%, 40%, and 60% intensities, in mid-summer, resulted in a 6.1%, 10.7%, and 11.9% decrease in IVTD, respectively, compared to the leaves, in 2006 (Fig. 4.19A). Sucker material clipped at 20% intensity was also more ($P \leq 0.000$) digestible than that clipped at 40% and 60% (4.5%, and 5.8% higher, respectively). Compared to the leaves, the difference in digestibility increased as the intensity of clipping increased in late summer. For example, suckers clipped at 20%, 40%, and 60% intensities resulted in a 6.6%, 8.8%, and 9.7% decrease ($P < 0.000$) in IVTD, respectively, compared to the leaves, in late summer. Also, clipping at 60% intensity caused a reduction ($P = 0.012$) compared to that clipped at 20% for this season.

In 2007, suckers clipped at 20%, 40%, and 60% intensities had a 7.3%, 8.9%, and 10.7% lower ($P < 0.000$) IVTD, respectively, than the leaves, in early summer (Fig. 4.19B). In addition, IVTD decreased ($P = 0.005$) by 3.4% for suckers clipped at 60% compared to those clipped at 20% for this season. Similar patterns were established by clipping in mid- and late summer in 2007 (Fig. 4.19B). Clipping suckers at 20%, 40%, and 60% intensities in mid-summer resulted in a 6.1%, 7.4%, and 8.6% decrease ($P <$

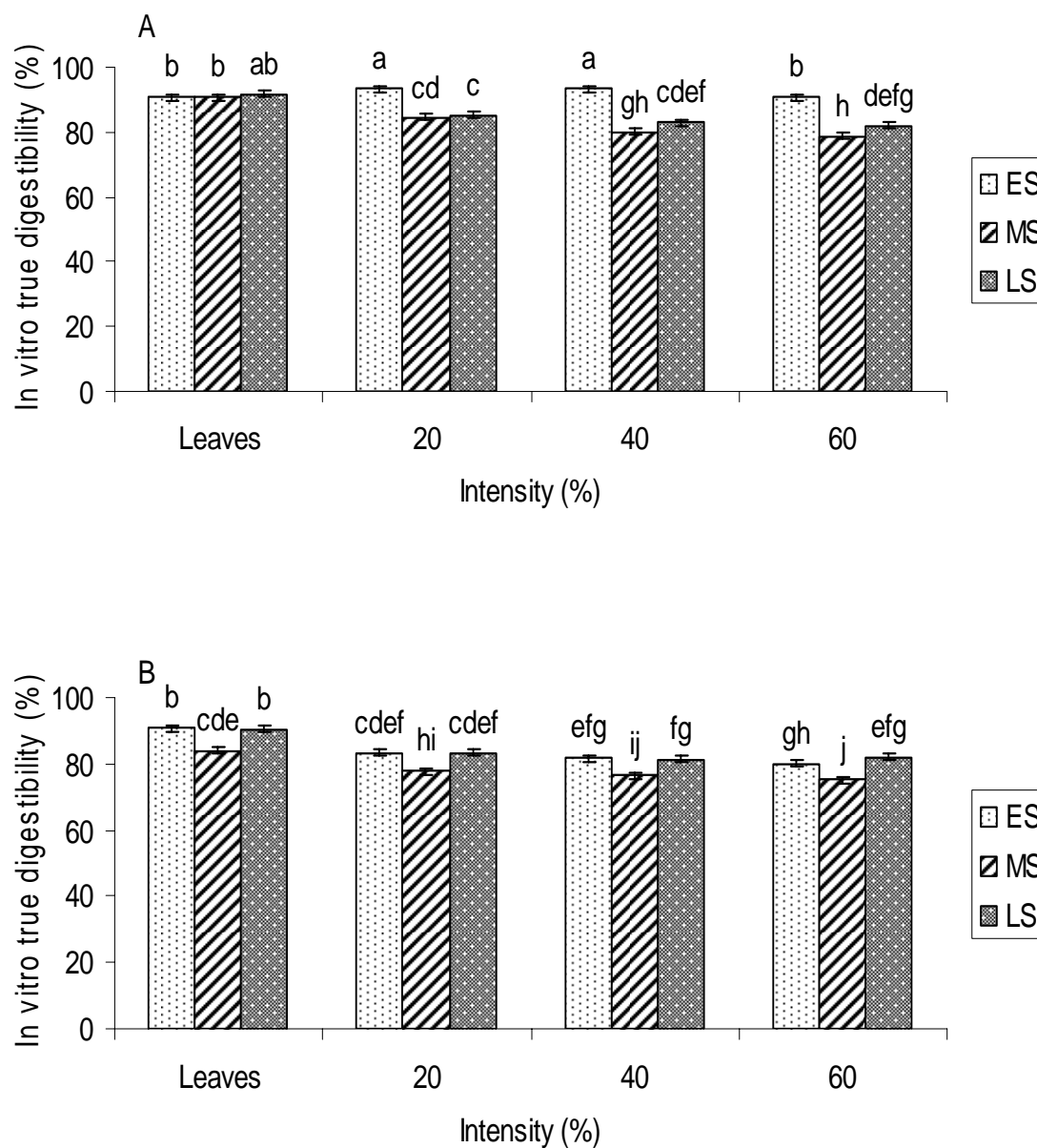


Figure 4.19. Mean in vitro true digestibility (%) of aspen leaves and aspen suckers clipped at different intensities and seasons in 2006 (A) and 2007 (B). ES = early summer; MS = mid-summer; LS = late summer. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

0.000) respectively, compared to the leaves. Clipping suckers at 60% intensity, in mid-summer, caused a 2.6% reduction ($P = 0.029$) in IVTD compared to clipping at 20% intensity. Also, material clipped in late summer at 20%, 40%, and 60% intensities resulted in a 7.1%, 8.9%, and 8.4% lower ($P < 0.000$) IVTD, respectively, than for the leaves.

Comparisons between years indicated no difference in IVTD for the control in early summer, but suckers clipped at 20%, 40%, and 60% intensities, were 10.0%, 11.6%, and 10.7% lower, respectively, in 2007 than in 2006 (Figs. 4.19A-B). Interestingly, in mid-summer, IVTD for the leaves was 6.8% lower in 2007 compared to 2006. Also, material clipped at 20%, 40%, and 60% were 6.7%, 3.6%, and 3.6% lower, respectively, in 2007 compared to 2006, for this season. This was not surprising as suckers accumulated more fibrous material as they grew. In late summer, even though IVTD of harvested sucker material was numerically lower in 2007 for all intensities, it did not differ statistically from that in 2006 (Figs. 4.19A-B). Interestingly, with the exception of suckers clipped at 20% in mid- and late summer in 2006, digestibility of clipped material in mid-summer was consistently lower than that for late summer in both years when comparing each clipping intensity. The results reported demonstrated a significant interaction between intensity x season x year in the ANOVA (Table 4.6).

Biomass, Total Digestible Dry Matter, and Total Nitrogen Harvested in 2006 and 2007

The season and intensity of clipping affected the amount of clipped biomass of suckers harvested from the site (Fig. 4.20A ; Table 4.7). Generally, clipped biomass increased substantially from 2006 to 2007 for early and mid-summer clipped plots,

Table 4.6. ANOVA fixed effects of season and intensity of clipping, and year on mean in vitro true digestibility values (%) of aspen suckers.

Source	Num DF	Den DF	F Value	¹ <i>P-value</i>
Season	2	4	77.33	0.001
Intensity	3	18	157.16	< 0.000
Season x Intensity	6	18	8.78	0.000
Year	1	24	173.05	< 0.000
Season x Year	2	24	28.90	< 0.000
Intensity x Year	3	24	4.00	0.019
Season x Intensity x Year	6	24	7.90	< 0.000

¹*P* -value considered significant at $P < 0.05$; ANOVA = analysis of variance; Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

except for late summer clipped plots that did not significantly differ between the years.

Clipping in early summer resulted in lower biomass than for mid- and late summer clipping in 2006, probably a reflection of the age and phenological stage of suckers when clipping treatments were applied. On average, biomass of suckers clipped at 20% (144 ± 15 kg/ha) and 40% (150 ± 15 kg/ha) was significantly lower than for 60% (222 ± 15 kg/ha).

Total digestible dry matter was affected by season, and intensity of clipping (Fig. 4.20B). Not surprising the amount of digestible dry matter removed by clipping followed the trends observed above for biomass. Total digestible dry matter increased for early and mid-summer clipped plots, but total digestible dry matter was not affected significantly by clipping in late summer between 2006 and 2007. Meanwhile, total digestible dry matter for suckers clipped at 20% (117 ± 12 kg/ha) and 40% (120 ± 12 kg/ha) was lower than for suckers clipped at 60% (175 ± 12 kg/ha). These results reflected a significant season x year interaction, and intensity effect for total digestible dry matter (Table 4.7).

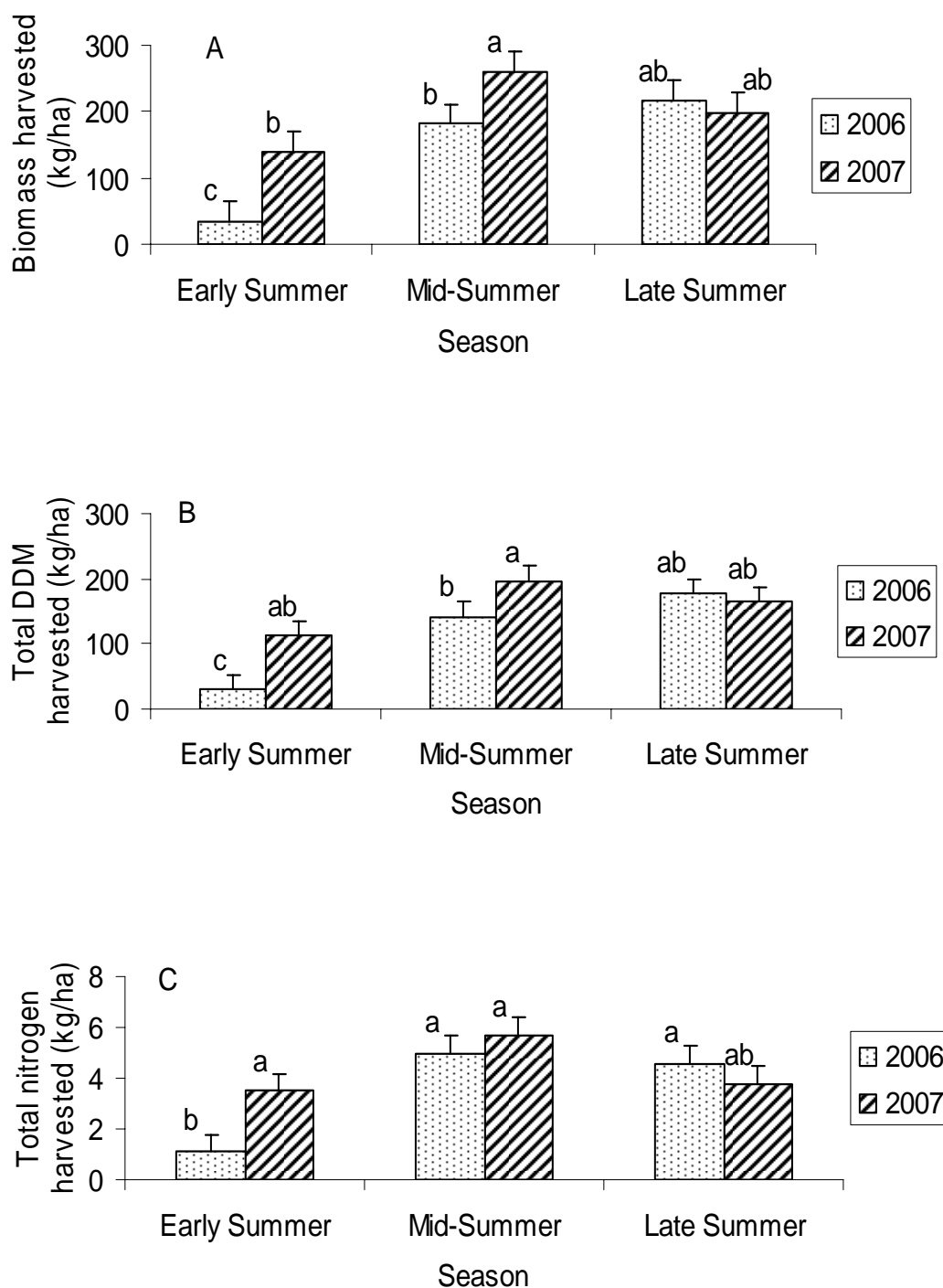


Figure 4.20. The effect of season on mean biomass (A), total DDM (B), and total nitrogen (C) harvested by clipping in 2006 and 2007. DDM = digestible dry matter. Means with different letters are significantly different at $P < 0.05$.

Table 4.7. ANOVA fixed effects of season, intensity of clipping, and year on biomass, total digestible dry matter and total nitrogen harvested in 2006 and 2007.

Source	Num DF	Den DF	F- Value	¹ P-value
Biomass (kg/ha)				
Season	2	4	6.37	0.057
Intensity	2	12	7.78	0.007
Season x Intensity	4	12	1.32	0.319
Year	1	18	9.38	<0.007
Season x Year	2	18	4.30	0.029
Intensity x Year	2	18	1.50	0.250
Season x Intensity x Year	4	18	1.07	0.401
Total DDM (kg/ha)				
Season	2	4	6.69	0.053
Intensity	2	12	6.67	0.011
Season x Intensity	4	12	1.03	0.433
Year	1	18	8.88	0.008
Season x Year	2	18	4.29	0.030
Intensity x Year	2	18	1.50	0.251
Season x Intensity x Year	4	18	1.00	0.432
Total nitrogen (kg/ha)				
Season	2	4	4.34	0.099
Intensity	2	12	7.08	0.009
Season x Intensity	4	12	1.38	0.299
Year	1	18	3.01	0.100
Season x Year	2	18	4.41	0.028
Intensity x Year	2	18	0.84	0.449
Season x Intensity x Year	4	18	1.09	0.389

¹P- value considered significant at $P < 0.05$; DDM = digestible dry matter; ANOVA = analysis of variance; Num DF, Den DF = numerator and denominator degrees of freedom, respectively.

Similarly, the season, and intensity of clipping significantly influenced the amount of total nitrogen harvested in clipped materials (Table 4.7). Except for early summer clipping, total nitrogen was not influenced differently by clipping in mid- and late summer between the two years (Fig. 4.20C). Consistently, as observed above, on average, clipping at 20% (3.3 ± 0.4 kg/ha) and 40% (3.4 ± 0.4 kg/ha) resulted in clipped

materials that were significantly lower in total nitrogen than those clipped at 60% (5.1 ± 0.4 kg/ha).

CHAPTER 5

DISCUSSION

Precipitation is considered one of the most important factors that influence aspen growth and development (Jones and DeByle 1985). Research has also shown that plants in high resource environments are most likely to respond positively to lost tissues compared to the same plants under poor environmental conditions (Bartolome 1993; Relva and Sancholuz 2000). In the present study, annual precipitation for 2005 and 2007 was well above the long term average, while 2006 was 10% lower than average (Fig. 3.1A). However, April to October precipitation, the period within which clipping treatments were implemented, was within that of the long term average for all years of the study. Temperature, a factor that is important for aspen regeneration and growth (Schier 1976) was also within the long term average for the area (Fig. 3.1B).

In this study, the interconnectedness and possibility of resource sharing among the suckers in clipped and adjacent untreated areas were not controlled. It is well documented that aspen suckers continue to get water and nutrients from the parent roots for some indefinite number of years (Zahner and DeByle 1965). Therefore, caution for interpretation and discussion in this document was exercised as reasonably as possible. None-the-less, results of this study should reflect the “real world” where herbivores selectively browse on newly-emerged suckers resulting from clear-felling treatments.

Sucker Density Responses

Sucker density in this study was affected by both season and intensity of clipping. Clear trends emerged that suggested that clipping in early summer was the least

detrimental to sucker survival compared to clipping in mid- or late summer (Figs. 4.1, 4.7, and 4.8). These trends are contradictory to conventional theory that suggests that clipping in early summer when carbohydrates are presumed to be at their lowest is detrimental to plant survival (Cook and Stoddart 1960; Willard and McKell 1978; Fitzgerald and Bailey 1984). My results support Hypothesis 1 (a) that clipping in late summer exposes suckers to winter kill more than does early summer clipping. It was difficult, though, to know exactly when these large changes in sucker density occurred for mid- and late summer treatments. Whenever this happened, it is reasonable to assume that winter conditions exacerbated the effects of clipping on the dynamics of sucker numbers for the two seasons. For aspen, clipping in early fall (late summer in the current study) stimulates shoot primordia to grow too late in the season to allow development of winter hardiness, and prevents shoots which had emerged earlier in the season from going into dormancy, leaving them susceptible to winter kill (Bailey et al. 1990). It seemed unlikely that the late summer clipped plots incurred carbohydrate exhaustion after just one clipping event, when suckers clipped early in the growing season (when carbohydrates are presumed low) escaped the winter with minimal mortality. Fitzgerald and Bailey (1984) observed that exhaustion of carbohydrates by annually repeated destruction of growing points required from six to eight years. I recognize that the treatments in this study may not have impacted carbohydrate reserves to the extent that severe natural browsing on entire stands would have, as my treatment plots were just spots within an otherwise intact stand. Therefore, the marked mortality for late summer clipped plots can be attributed to death of suckers due to the cold. Actually, substantial numbers of dead suckers were observed in mid- and late summer clipped plots during

sampling in summer of 2007. These results are consistent with other research findings in Canada on timing of browsing on aspen. For example, Fitzgerald and Bailey (1984) observed that pastures browsed in early summer (June) had 29% aspen, compared to 2.5% aspen for pastures browsed in late summer (August). These results were reported one year after the treatments were implemented. I also found that intensity of clipping did not significantly affect over-winter survival of suckers, leading me to reject Hypothesis 1 (b) that stated that increased intensities of clipping would result in increased winter mortality. This finding probably further demonstrates aspen's substantial tolerance to tissue removal.

Previous research indicates that sucker densities typically peak in the first or second year after disturbance, then decline rapidly in subsequent years (Schier and Campbell 1978). Several factors, including root wounding from the clear-felling process, promotes suckering (Fraser et al. 2004). In this study, dragging of logs when the sites were cleared probably contributed to root wounding, leading to considerable suckering in the summer of 2005. Because the perimeter fences were taken down in late fall of 2005, due to fear of their being destroyed by the weight of snow, all of the suckers that had emerged in summer of 2005 were lost to deer and elk browsing during late winter/early spring of 2006. Thus in the summer of 2006, the stands were suckering for the second time since the tree stands were felled. As a result, fewer new suckers that might have otherwise had influence on the dynamics of sucker numbers were observed after the clippings were implemented. Perhaps it is worth noting that survival of the remaining suckers after browsing and natural thinning is crucial, because about two cycles of suckering and browsing is about as much as aspen seem to tolerate.

When comparing rate of change in sucker density within years, patterns emerged suggesting that early summer clipping resulted in high sucker mortality by the end of the (first) current growing season (2006) compared to mid- and late summer, in that order (Fig. 4.14B; Figs. E.10A-C), supporting my Hypothesis 1 (c) that clipping is more detrimental to sucker survival when done in the first growing season compared to the second growing season. In early summer of 2006, the suckers had just resumed growth, and most of them had emerged during spring and summer that year, making them even more susceptible to clipping. As expected, as the canopies of suckers expanded in 2007, their ability to tolerate clipping increased, and the effects were not different between seasons (Fig. 4.14B). These results seemed to support the notion that bigger plants have a more developed photosynthetic surface area and can better withstand some level of clipping than can young, small plants (Boege and Marquis 2005).

It is generally recognized that aspen mortality is highest during the first five years after the parent trees are harvested (Bartos et al. 1991), due to competition for nutrients or carbohydrates (reviewed by Frey et al. 2003), among other factors. Perhaps it is worth noting that suckers get resources from the roots of parent plants. This interconnectedness allows suckers to directly compete with each other for resources. In the first growing season (2006), death of suckers was highest regardless of the intensity of clipping (Fig. 4.14A), supporting in part my Hypothesis 1 (c) that clipping in the first growing season is detrimental to sucker survival compared to the second growing season. Comparing the rate of change for the clipped plants and the controls, it was unlikely that most of the suckers died due to self thinning. Additionally, studies have documented that herbivory can be most detrimental at the early stages of growth (Garrison 1963; Bergström and

Danell 1987), because plants invest much of their root resources into carrying out the physiological processes (e.g., photosynthetic surface area creation), required by suckers (reviewed by Frey et al. 2003). Therefore, removal of foliage during this period further constrains the plant. Typically, in this study, some suckers were observed to have a progressive dieback after being clipped, and those suckers eventually died by the end of the current growing season, especially in 2006.

Despite the fact that late summer clipping reduced sucker density relative to early summer clipping, the magnitude of the decrease was not of concern with respect to potential regeneration of the stand. Actually, late summer treated plots that suffered the highest mortality had 20,444 suckers/ha by the end of the study. Research has shown that an aspen stand will most likely fail to regenerate and sustain itself if the density of well-formed stems falls below 1,250 stems/ha (Bartos and Campbell 1998a). From an aspen stand management standpoint, sucker densities at the end of the current study, for all clipping seasons, were still high enough to ensure sustained stand regeneration.

Sucker Growth Responses

Early season herbivory is generally easier to compensate for in established plants, whereas immature and seedling plants can be poor tolerators of early season herbivory (Strauss and Agrawal 1999). One year after clipping, early summer clipped suckers were significantly shorter than the controls for all clipping intensities (Fig. 4.2B), while leader length for clipped suckers was not different from the controls (Fig. 4.3B). With regard to intensities, clipping at 20% and 40% in mid- and late summer seasons did not affect sucker height relative to the controls, but suckers clipped 60% were shorter (Fig. 4.2B).

Leader length was stimulated by mid- and late summer clipping (Fig. 4.3B). These trends seem to support my Hypothesis 2 (a) that stipulated that early summer clipping is more harmful to sucker growth than mid- and late summer clipping; and Hypothesis 2 (b) that clipping limits sucker growth as the intensity of clipping increases.

Lindroth (2001) noted that tolerance is a viable form of defense in plants with high intrinsic growth rates, large storage capacity, and high rates of photosynthesis, all traits of aspen. Other researchers, e.g. Hewett and Wareing (1973) have hypothesized that increased growth after tissue loss may be a result of increased cytokinin levels in residual tissue, thus allowing compensation to occur. Research on aspen has also shown that suckers having good competitive advantage can reach heights of 1 m within a single growing season (Jones and Schier 1985). Julander (1937) studied the effects of ungulate browsing and clipping on quaking aspen sucker heights and found that suckers browsed or clipped > 75% of current year's growth showed a decrease in height. In contrast, Campa et al. (1992) observed no difference in sucker heights clipped at levels of 25%, 50%, and 75%. However, a major procedural difference from my study was that they severed all roots around their treatment plots to a depth of 31 cm. This was observed to be the maximum rooting depth of aspen parent roots in the Lake States where the study was done (Schier et al. 1985). Additionally, unlike the present study, their clipping was done in February, a period when nutrients in twigs are considered to be at their lowest levels (Alban 1985), as opposed to high nutrient loss associated with summer clipping (Bryant et al. 1983). This suggests a major penalty for suckers clipped at 60% in my study.

Another factor to consider is that heavily browsed suckers may be placed at a competitive disadvantage if associated plants of other species are not browsed or grazed and grow up to over-shade the browsed suckers (reviewed by Belsky 1986). However, under normal environmental conditions (e.g. adequate moisture, sunlight) herbaceous plants appear to have no appreciable effect on aspen sucker growth (Mueggler 1989; D. L. Bartos, personal communication, January 2008). In the present study, associated vegetation never exceeded the heights of suckers. Romme et al. (2005), researching the effects of clipping (levels not specified) on aspen sucker growth, observed no significant effect of herbaceous vegetation on sucker height growth in Yellowstone National Park. Whatever the reason might be, the weight of the evidence suggests that browsing aspen suckers at 60% intensity in mid- or late summer year-after-year can not be sustained.

After two consecutive years of clipping, sucker height growth was reduced by clipping relative to the control, with the reduction tending to increase as the intensity of clipping increased (Fig. 4.9). Similar findings were reported by Puettmann and Saunders (2001), who observed no compensation, and growth decreased sharply with increasing clipping intensities after one growing season for white pine seedlings in Minnesota. In yet another study, Bergström and Danell (1987) reported that heights of birch plants usually decreased with increasing clipping intensity.

Responses to herbivory may differ between years depending on the stage of plant growth when browsed (Maschinski and Whitham 1989). In the current study, intensity and season of clipping affected sucker height growth dis-similarly (Figs. 4.15A-B) and leader length (Figs. 4.16A-B) in both years. Perhaps it should not be surprising that suckers gained some height growth and leader length after being clipped in early summer

of the first year, but that they did not grow as much in the second year, leading me to reject in part my Hypothesis 2 (c) that says sucker growth will be restricted more in the first growing season than in the second growing season. Zahner and DeByle (1965) noted that continued rapid growth of suckers indicated that the large, well-developed parent roots serve significantly in water and nutrient absorption for some time. The year 2007 was fairly wet (Fig. 3.1A) and soil conditions for plant growth were probably not limiting. Actually, soil moisture content was relatively higher in early summer than either mid or late summer in 2007 (Table B.2), as the result of recent snow melt. If indeed, the marked decrease in growth for control suckers in 2007 was not moisture related, it may have been the result of photosynthate being allocated to below-ground root development (Jones and Schier 1985). However, if that were the case, then the clipped suckers would presumably have behaved likewise; instead, they demonstrated a rapid re-growth in the second year (as noted above). Other researchers have asserted that browsed trees grow in a such way as to re-establish the pre-browsed root/shoot ratio (e.g. Bergström and Danell 1987).

By study's end, neither the control nor the clipped suckers had attained the postulated browse height of 1.5 m necessary to escape terminal leader browsing (Smith et al. 1972; see Fig. 4.9). Monitoring terminal leader growth is important for the management of aspen suckers, for it is the region of elongation year-after-year (Keigley and Frisina 1998), and it defines whether a plant gains sufficient height to escape browsing. Although I observed that mid- and late summer clipping stimulated sucker height growth and leader length in the following year, browsing this late may unduly expose suckers to winter kill.

Browsing may stimulate branching of plants, due to broken apical dominance (Schier 1976), thus releasing lateral growing points from inhibition, and increasing the growth and fitness potential of the plant (Maschinski and Whitham 1989). In the current study, twig density, an indicator of branching, tended to decrease as the intensity of clipping increased (Figs. 4.4A and 4.11A), and more twigs were present in early summer treated plots than in mid- and late summer treated plots, especially in the second year (Figs. 4.4B and 4.11B). Guillet and Bergström (2006) observed a decrease in the number of twigs on willow (same family as aspen) plants with increasing (summer-time) clipping intensity. Although twig density decreased as the intensity of clipping increased, twig density was higher in early summer than in mid- and late summer. As noted above, early summer clipping gave suckers enough time to re-grow and presumably replenished resources before the dormant season began. Because of broken apical dominance and adequate energy, it seemed reasonable that many buds opened up resulting in many twigs being produced. Though mid- and late summer 2006 clipped suckers had a significant increase in twig density from time B06 to B07, the increase was not so pronounced as that for the early summer treatment. Clipping for these seasons came much later in the season and probably did not give suckers enough time to replenish the resources before the growing season ended. Arguably, this then implied that resources were probably limited at the beginning of the growing season the following year. With inadequate resources, it seemed reasonable that the suckers devoted more resources to height growth (as shown earlier) for these seasons, and less into lateral expansion. Furthermore, these trends could be due to less mortality for early summer treated plots compared to mid- and late summer treated plots. Some researchers have observed that willow plants invest

more into compensatory growth after early summer browsing, as opposed to defense after late summer browsing (e.g., Herder et al. 2004). Other studies have also shown that fast growing plants invest more into growth at a young age than into defense (reviewed by Coley et al. 1985). This response is presumably geared to creating and replacing the photosynthetic surface area lost to herbivory early in the growing season rather than later in the season when plants can better withstand some level of browsing.

Usually, browsing affects seasonal changes in bud production on plants (Klimešová and Klimeš 2007). Increased bud production can be a viable mechanism deployed by plants in response to browsing (Tuomi et al. 1994), as buds are responsible for the ultimate expansion of the photosynthetic surface area and subsequently growth of plants (Klimešová and Klimeš 2007), thus providing the basis for compensation to occur after tissue loss. Not surprising, bud density in the present study tended to follow similar patterns displayed by twig density, because buds are produced on twigs. Bud density decreased as the intensity of clipping increased (Figs. 4.5A and 4.12A). For reasons advanced above in terms of resource availability, early summer clipping allowed for more bud recruitment than did mid- and late summer clipping (Figs. 4.5B and 4.12B). Bergström and Danell (1987) observed increased total numbers of buds on whole trees of birch plants with increasing intensity of clipping, but the number of buds decreased on the new twigs that emerged after the clipping treatment.

Classically, tree basal area is used as a measure of site occupancy in forest management (Jones et al. 1985b). In this study basal area growth was affected by both season (Figs. 4.6 and 4.13) and intensity of clipping (Fig. 4.17). In general, basal area growth tracked sucker density changes. By the beginning of the second growing season,

basal area for suckers clipped in early summer (2006) was similar to mid- and late summer (2006) clipped suckers and had roughly doubled in amount from that observed one year earlier. This finding could be attributed to minimal or no winter mortality for early summer clipped plots than for mid- and late summer clipped plots that experienced considerable mortality (see sucker density). These trends in basal area growth were not surprising, since diameter growth for aspen suckers usually increases considerably with reduced competition for resources among suckers, as a result of mortality (Jones et al. 1985b).

In the first growing season, clipping was detrimental to basal area growth regardless of intensity compared to the control (Fig. 4.17), refuting my Hypothesis 2 (b) that clipping limits growth more as the intensity of clipping increases. These results were consistent with other clipping studies on woody plants. For example, Saunders and Puettmann (1999) reported reduced diameter growth (implying reduced basal area growth) for white pine seedlings clipped at 50% and 100% of current year's growth compared to the control. However, with passing time, even though browsing continues, basal area usually increases (DeByle 1985; Keigley and Frisina 1998), but sucker height may be restricted. Comparison between years indicated that basal area growth was not affected differently by clipping leading to rejection of Hypothesis 2 (c) that clipping limits sucker growth the most when done in the first growing season rather than in the second growing season. Conversely, basal area growth for the control was significantly higher in 2006 than in 2007, probably an indication of adjustment in root/shoot ratio as the suckers aged (Jones et al. 1985b; Campa et al. 1992).

Nutritional Responses

For plants to cope and tolerate herbivory, they have to be able to replace carbon and other nutrients associated with tissue loss. Studies have demonstrated that early summer browsing decreases nitrogen concentration in leaves of browse trees in the next summer, while late summer browsing has the opposite effect, at least for one year (reviewed by Danell et al. 1994). However, *repeated* browsing in late summer tends to decrease nitrogen concentration (reviewed by Danell et al. 1994). Therefore, late summer browsing could be deleterious from the standpoint of plant growth and development. On the other hand, winter browsing has been found to increase fiber concentrations the following year (Danell et al. 1985; Danell and Bergström 1989). From the standpoint of the herbivore, these changes can have important implications. For aspen systems where multiple resource use is of interest, it is appropriate for resource managers to be able to quantify the effects of herbivory in terms of tissue loss to browsing and what the plant can tolerate. Likewise, changes in plant traits as a result of browsing (e.g. biomass, amount of twigs, buds, etc.) will have direct consequences for subsequent nutrition of browsing herbivores in terms of such nutritional factors as crude protein concentrations and digestibility (i.e. fiber content).

Crude Protein Content. In general, forage plants are high in crude protein early in the growing season, and then decline in this component as the growing season progresses (Kubota et al. 1970; Cook 1971; Palo et al. 1985). The results for the present study indicated that, true to this generalization, crude protein generally decreased as the growing season progressed (Figs. 4.18A-B). Kubota et al. (1970) and Tew (1970b) reported such trends in crude protein content through the summer months for quaking

aspen in Alaska and Utah, respectively. Surprisingly, mean crude protein for leaves plucked from nearby suckers was lower ($P \leq 0.017$) than for the clipped suckers in early summer of 2006 (Fig. 4.18A). There appeared to be no substantial reason for this observation, because clipped samples always contained some amount of stem material, albeit very little in early summer. However, though unlikely, this pattern could be attributed to the fact that materials clipped contained substantial amounts of buds, a potential place for nitrogen accumulation. Studies have also documented substantial movement of nutrients between the growing points (e.g., buds, leaves) and the perennial tissues (e.g., bark) of deciduous trees (e.g., Chapin et al. 1975; Chapin and Kedrowski 1983). Therefore, the lower crude protein content in leaves may have reflected a time effect, suggesting that nitrogen was not yet fully mobilized from the perennial tissues to leaves in early summer.

There is a tendency for nutrient concentrations in plant material to decline as the level of utilization by animals increases (Oelberg 1956; Cook and Harris 1968). In the current study, mean crude protein appeared to decrease as the intensity of clipping increased for all seasons in 2006 (Fig. 4.18A). However, no comparable differences were noted for all clipping intensities within a season in 2007 (Fig. 4.18B). Other studies have noted that herbivory may alter nutrient cycling in plants (e.g., Dyer 1975). In fast growing species, with large storage carbon reserves and high photosynthetic rates, leaf removal signifies loss of nutrients. Where excess carbon cannot be used for growth it will accumulate as carbon-based secondary metabolites (Bryant et al. 1983). Such fast growing species have been observed to have less nitrogen in the foliage the year following a severe defoliation (Bryant et al. 1991). Generally, mean crude protein

content of suckers in 2007 was significantly lower than those for 2006 for all clipping intensities and across seasons. The results for year two were in agreement with those of Campa et al. (1992) who observed no difference in crude protein content between clipped plots and the control for quaking aspen twigs after two years of simulated browsing. Many studies have observed that forage nutrients are diluted by structural carbohydrates as the plant matures (e.g., Short et al. 1974), and as intensity of utilization increases (e.g., Oelberg 1956; Kamstra et al. 1958; Short et al. 1974). In the present study, the lack of a significant difference in 2007 between plucked leaves from off-plot suckers and leaves plus stems from the clipping treatments within a season, suggested that clipping intensity was probably not much of a contributing factor in influencing crude protein content at any particular time. This might be attributed to the growing habit of suckers re-distributing resources below-ground for root development, rather than to above-ground allocation as the canopies expanded (Campa et al. 1992).

Though chemical analysis is not an absolute measure of the nutritive value of range forage, it does provide a relative index to the nutritional value among species and the effect of utilization intensity during different seasons of the year (Cook 1971). Previous work by Ullrey et al. (1967) reported that dietary protein levels significantly influenced body weight of white-tailed deer fawns in Michigan. In the present study, mean crude protein content of suckers (17.3%) would largely meet the nutritional requirements of adult deer (6-9%) (Ullrey et al. 1967; Mould and Robbins 1981), and growing deer (12-16%) (French et al. 1956) in the first year after clear-felling. However, in the second growing season (2007) mean crude protein of suckers (< 11.8%) failed to meet the requirements for growing deer. This was especially the case for the leaves and

the 40%, and 60% clipping intensities in late summer. Although the winter months are considered critical for survival of cervids (Ullrey et al. 1967), the summer months can also be nutritionally important for wild ungulates (Renecker and Hudson 1988). This is the time when body condition must be re-gained in a short period of time to ensure successful reproduction, growth and over-winter survival. The results for the current study suggested that growing deer would not meet their late-summer protein requirements in the second year post-clear-felling if aspen suckers are the most protein-rich forage available. These findings probably further provide some insight into why both deer and elk consume more suckers but less notably so for leaves of mature aspen trees. Perhaps, it is worth noting that at crude protein content $> 17\%$, aspen suckers provide higher levels of crude protein than any of the associated species in the plant community, especially considering the fact that these landscapes no longer support the protein-rich forb component that they once did. In fact, Ruyle (1983) analyzed the diets of sheep grazing Cedar Mountain ranges and reported dietary crude protein levels not exceeding 12% at any time during the summer.

Domestic livestock, especially sheep, utilize substantial amounts of aspen suckers on Cedar Mountain (Lucas 1969; Davis 2007) as well as on other high-elevation ranges across the West. In the current study, crude protein requirements for maintenance (9.4%) and flushing (9.1%) of 70 kg sheep (Jurgens 2002) were met by leaves and materials clipped at all intensities in both years. However, crude protein requirements for 70 kg ewes (13.4%) suckling single lambs and for 30-kg finishing lambs (14.7%) (Jurgens 2002) were not met by leaves or by browse clipped at 40% and 60% intensities in late summer of year two. From a personal observation, ewes with lambs utilized Cedar

Mountain range throughout the summer months for the entire duration of the study.

Therefore, mean crude protein fluctuations during late summer in year two could limit sheep production on this range. Davis (2007) observed considerable use of Crystalyx dehydrated molasses-protein supplement by deer and elk on Cedar Mountain, as well as by the cattle and sheep for which it was intended, suggesting in part that their nitrogen requirements were probably not being met by the general mix of forages on this range. He also observed considerable combined usage (49% by late summer) by deer and elk (he was unable to distinguish between the two) of aspen suckers that appeared within intact aspen stands. However, the abundance of these suckers was many-fold less than would be found in a clear-felled stand such as mine.

In Vitro True Digestibility. Analyses of material from the clipping intensities indicated that IVTD generally decreased as the intensity of clipping increased within a season (Fig. 4.19A-B). This was consistent with many other studies that have documented that digestibility typically decreases as the intensity of utilization increases (Oelberg 1956). In the free-ranging animal, this is generally the result of an increase in fiber content of harvested material. Apart from the hand-plucked leaves that did not differ between seasons, digestibility in year one was highest in early summer compared to other seasons. Moisture content of forages typically decreases as the growing season advances, and plants with high moisture content usually have less fiber and lignin and are highly digestible (Sullivan 1962). In 2006, moisture content of harvested materials averaged about 68% for early-summer-clipped plots compared to 61% for late-summer-clipped-plots. Unexpectedly, IVTD for the leaves (89.9%-91.8%) was slightly lower

than for the 20%, and 40% clipping intensity in early summer. This finding was consistent with the lower crude protein content of leaves observed above.

There was a moderate decrease in IVTD for the clipping intensities compared to the leaves for all seasons in 2007 (Figs. 4.19B). This was not surprising because of the relatively lower fiber content in leaves than in twigs of suckers. Unexpectedly, however, IVTD for mid-summer clipped materials was for the most part lower than for late summer clipped materials in both years (Figs. 4.19A-B). Forage nutritive composition at the time of harvest is the cumulative result of plant growth and the environmental factors influencing the distribution of photosynthetically derived energy and nutrients in those plants (Van Soest et al. 1978). Additionally, concentrations of soluble carbohydrates have been observed to change depending on the time of the year for deciduous trees (Wong et al. 2003). For example, Wong et al. (2003) observed high levels of soluble sugars in senescing leaves of sugar maple (*Acer saccharum* Marsh.) in September, a period that corresponds with my late summer clipping. They attributed the high levels of soluble sugars to the possibility of degradation of glycosidic compounds (e.g. anthocyanins and aromatic amino acids) and numerous other compounds (e.g. lipids and protein) to sugars during autumn (Kramer and Kozlowski 1979), suggesting overall increase in digestibility of harvested materials. Actually, McCullough (1979) observed an increase in digestibility of aspen leaves and twigs by addition of carbohydrates (cornstarch).

A comparison between years indicated differences in IVTD within the clipping intensities for early and mid-summer clipped materials, with late summer clipped materials tending to be lower in 2007 than in 2006, though not statistically different

(Figs. 4.19A-B). These results should not be surprising as suckers were growing, aging, and accumulating more fibrous structural material (Oelberg 1956; Johnston et al. 1968; Cook 1971).

Research has shown that digestibility can be used as an integrative measure of forage quality for ruminant animals (Cook and Harris 1968). Therefore, low forage digestibility may seasonally limit vertebrate populations on landscapes (Chen et al. 1998). For example, Blaxter et al. (1961) reported that for sheep an increase in diet digestibility from 50% to 55% increased body weight gain nearly 100%. Therefore, small differences in diet digestibility would likely result in large differences in animal condition (Baker and Hobbs 1982). However, in the present study digestibility of harvested materials were very high (> 70% for all seasons) in both years (Fig. 4.19A-B). It should be noted that the values observed in the present study are substantially higher than the literature values presented in Table 2.2 partly because those are in vitro dry matter digestibilities (IVDMD) instead of IVTD values. Even considering the difference, values appear to be exceptionally high, considering that IVDMD (apparent digestibility) is usually about 12.9 digestibility units lower than IVTD values (Ghadaki et al. 1975). Research has also shown that IVDMD obtained by the Daisy^{II} Incubator (ANKOM Technology) that I used can vary for some feedstuffs. For example, Mabjeesh et al. (2000) reported a 17% and 21% higher IVDMD from the Daisy^{II} compared to the Tilley and Terry method for sunflower meal and alfalfa cubes, respectively. Several factors have been advanced for this discrepancy. For example, the porosity of the F57 sample bags and the sample size per unit of bag surface area may affect the results (Nocek 1988; Vanzant et al. 1998; Mabjeesh et al. 2000) for forage materials.

Additionally, sample processing, particularly grind size, interacts with pore size of the bag and affects the extent of material disappearance (Mabjeesh et al. 2000). Unlike, in my study, Mabjeesh et al. (2000) used a 2-mm pore-size Willey mill screen for grinding the samples while I used a 1-mm screen. On the other hand, the standard grass hay I used had IVTD values that closely approximated (4% lower) values established at the Utah State University Skaggs Laboratory. Therefore, the higher digestibility values observed in my study may represent a systematic bias due to escape of indigestible materials through the pores of the F57 bags during digestion in the Daisy^{II} Incubator and also in the neutral detergent fiber procedure.

Biomass, Total Digestible Dry Matter and Total Nitrogen Harvested in Aspen Suckers

The season and intensity of utilization of range plants are important considerations in a browsing management program to ensure that both plant health and animal productivity are sustained (Cook 1971; Holechek et al. 1998). In this study, although season by intensity by year interaction was not significant, clipped biomass increased from 2006 to 2007 for all seasons and intensities. Meanwhile, browsing management principles suggest browsing later in the growing season because plants then have a larger photosynthetic surface area to better withstand some level of browsing (Holechek et al. 1998). In contrast to these browsing principles, harvesting aspen in early summer did not significantly reduce biomass, total digestible dry matter and total nitrogen harvested per ha compared to late summer harvesting, especially in 2007, due in part to lower sucker mortality over winter in early summer-clipped suckers. These results

suggest that browsing herbivores would potentially benefit similarly in terms of harvestable biomass when browsing in early or late summer in the second year. Previous research on management of ranges suggests that mid-summer browsing favors subsequent plant growth because carbohydrates are presumed highest then (Holechek et al. 1998), suggesting less impact on suckers browsed at that time. From a browse management perspective, these trends suggested that in terms of sustained plant vigor (growth) and high biomass harvestable by herbivores, mid-summer browsing achieved both of these objectives.

From the standpoint of browsing (clipping) intensity, on average, harvested biomass for 20% (lightly) and 40% (moderately) clipped plots was lower than biomass for intensely (60%) clipped plots, suggesting, in part, that intensely clipped suckers were also stimulated and made-up for lost biomass. Because harvested biomass for intensely clipped plots was significantly higher than for the two lesser intensities, the 60% clipping was probably not intense enough to surpass the maximum level of browsing beyond which suckers would not be stimulated, as suggested by the grazing optimum hypothesis (Belsky 1986). These results of increased biomass production after experiencing tissue removal are supported by previous work by Julander (1937) who reported increased total biomass production for aspen clipped $< 75\%$, and they further demonstrate the plant's ability to persist and reproduce while sustaining moderate to heavy levels of browsing.

The high biomass, total digestible dry matter, and total nitrogen harvested may largely explain the browsing patterns we see on Cedar Mountain and elsewhere. It has long been hypothesized that forage use by ungulates can be influenced by a number of factors (Kenney and Black 1984). For example, Belovsky (1997) noted that herbivores

may use two criteria (a maximum digestibility and a maximum cropping rate) in maximizing their nutritional intake when confronted with a range of food resources. Other researchers have noted that the intake rate of forages depends upon (i) the potential rate at which it can be eaten, (ii) its accessibility, and (iii) its relative acceptability (Kenney and Black 1984). Furthermore, the potential rate at which a feed component can be eaten is determined largely by the physical characteristics of the feed, such as its ease of fracture, size particles and water content (Kenney and Black 1984). However, the size of the animal's mouth, its degree of satiation, and its physiological state may also be important (Ellis 1978; Kenney and Black 1984; Milne 1991). Therefore, the relatively high moisture content and digestibility of suckers observed in this study may partly explain the extensive ungulate browsing observed on Western landscapes. Additionally, aspen suckers are usually easily accessible in nature because of the occasional clumps that they form when emerging from the soil. As such, this clumping of suckers presents an opportunity for the animal to maximize intake with minimal foraging time. Studies have shown that free-grazing animals have the capability of selecting for forages with relatively high nutrients that they require (Ozanne and Howes 1971). For example, Ozanne and Howes (1971) observed that sheep grazing dry pasture selected for material with a high phosphate content. The positive relationship between animal selectivity and plant nitrogen content is also well established.

Additionally, aspen communities provide shade, good foraging grounds and cover for both wild and domestic animals, especially during the hot summer months. As research has shown, aspen systems contain the highest species diversity of all upland plant communities (Bartos and Campbell 1998a), and because of shade provided by the

aspen canopy, associated vegetation grows late in the season, providing green forage to ungulates. Because of these factors, the likelihood of aspen suckers being selectively browsed is extremely high.

Management Implications

Western landscapes are home to both domestic and wild ungulates. As has been observed (in this study), aspen suckers produce considerable amounts of potential forage that is highly nutritious. Browsing these suckers would obviously improve the diets of free ranging animals during the summer months. Meanwhile, efforts to restore aspen are faced with two major problems, i.e., the large herds of native ungulates (deer and elk) and domestic livestock that can lead to over-browsing. Therefore, from an aspen restoration standpoint, it requires that we regulate use on aspen suckers by these ungulates. Practically, the only herbivore that can easily be controlled is sheep. Because fencing of treated aspen stands to exclude deer and elk is usually prohibitively expensive, about the only current option is to follow the recommendations of Bartos and Campbell (1998a). Specifically, for any clear-felling program to successfully regenerate aspen in the presence of deer and elk, areas larger than 200 ha should be done to spread the browsing on suckers beyond the ungulates' capability to destroy the response. Additionally, several (on-site) methods to curb the problem of over-browsing on aspen suckers have been tried in other parts of the United States, with appreciable levels of success. For example, Kota (2005) found that the hinge and slash treatment methods can be successful at deterring livestock, deer, and elk from accessing and browsing aspen suckers in the Black Hills of South Dakota. He further noted that the hinge treatment provides better

protection of suckers at a less cost than fencing, such that larger areas can be treated.

Where cattle are the main browsers of aspen suckers, Kota (2005) further suggested that a slash barrier will result in the same outcome as a livestock fence, but at a lower cost.

Because most of the aspen-growing public lands are permitted out to ranchers for livestock grazing, it is critical that ranchers are involved right from the initial planning phase. From a rancher's point of view, summer range grazing is typically crucial for his year-long livestock enterprise. As such, he likely would not be willing to agree to give up all or part of his grazing permit to rest recently treated pastures. However, compromise solutions may be possible.

Because sheep are of greater concern for use of aspen suckers than are cattle on high-elevation, southern Utah rangelands, I hereby propose a clear-felling program involving sheep grazing. Based on the findings of this study, browsing at intensities $\leq 40\%$ in mid-summer would ensure sustained aspen stand development. As noted above, managing aspen on landscapes is hampered by both native and domestic livestock. I recognize that clear-felling operations increase the risks of over-browsing by both these species of animals. Therefore, the 40% tolerable level in mid-summer should be the total maximum browsing allowable by both native and domestic animals. Meanwhile, current Forest Service guidelines call for removal of livestock from treated pastures when use on suckers reaches 20% (D. L. Bartos, personal communication, March 2005). Even though considerable numbers of suckers were lost when treatments were applied in mid- and late summer, sucker numbers were still high ($\geq 20,444$ suckers/ha) for all seasons of clipping by the end of the second growing season. Therefore, mid- and late summer clipping appeared to be the best times for the treatments to be implemented. Meanwhile,

monitoring is important to document the progress of the grazing program. Therefore, it is important that small exclosures be created in all clear-felled stands to serve as control plots to monitor the effects of sheep browsing on the suckers. Three possible scenarios for the management of pastures that have recently been clear-felled are proposed:

Scenario A. In areas where season-long grazing is practiced, as it is on most Forest Service lands, it will be difficult and financially costly for ranchers to rest the treated pastures altogether. Therefore, because most growth of suckers would have occurred by the end of July, sheep grazing should be delayed for at least two months (June and July) until the beginning of August in the year following the clear-felling operation. This deferred grazing should allow suckers time to grow and harden off (Dockrill et al. 2006), thus minimizing the impacts of browsing. However, because of the unpredictable nature of weather conditions, it is critical that strict adherence to grazing capacity of the pastures is observed as close as possible.

Because of the additional (and highly nutritious) forage provided by suckers in the years following clear-felling operation, the rancher might be cautiously permitted to increase his stocking rate as a reward for giving up his grazing permit in the early part of the summer grazing season. It is important though, that this grazing arrangement is adhered to for at least five growing seasons before the normal grazing schedule gets back in place. Presumably, by the end of the fifth growing season suckers will have grown and passed the 1.5 m safe height. Additionally, it is critical that a monitoring protocol (e.g., sucker density, sucker height, leader length) be developed to ensure that aspen stand replacement is not compromised.

Scenario B. For aspen ranges where deferred-rotation (Sampson 1913)

grazing programs are in place, it may be easier to clear-fell multiple pastures at a time or in subsequent years. When clear-felling in subsequent years, again delaying grazing on the treated pastures the year following clear-felling operation for at least two months during the summer growing season is critical. Because the rancher and the range manager have an option of when and where to graze (due to multiple pastures), it is important that sheep do not graze the same pasture at the same time in successive years. Assuming a grazing program involving two pastures for the summer growing season, the pasture that would have been grazed first in the first year following clear-felling should be grazed last in the second year. This arrangement ensures that suckers in both pastures get some time to re-grow at least for part of the growing season after being browsed. The grazing process should be adhered to until terminal leader of suckers are out of reach of sheep. Again, a monitoring protocol on suckers should be adhered to at all times.

Scenario C. In addition to grazing strategies suggested under scenarios A and B, where there are small areas occupied by aspen (i.e. small clear-felling operations), it may be necessary to put supplements at strategically placed areas away from the treated stands to encourage better sheep distribution in the pastures. Additionally, where supplementary feeding is not possible, herding sheep away from the treated stands from time to time may be required to encourage better animal distribution.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Summary

During 2006 and 2007 a simulated browsing study was conducted on high-elevation range of southern Utah to determine the effects of three seasons (early, mid- and late summer) and four clipping intensities (0%, 20%, 40%, 60%) on aspen sucker density and growth characteristics. Three aspen stands were randomly selected and clear-felled in mid-July of 2005. These stands were fenced with a 3 m-high game fence to protect suckers from being browsed. Clipping treatments were imposed on suckers in the summers of 2006 and 2007 on permanently demarcated plots. Data were collected on sucker density, height, leader length, twig density, bud density and basal area of suckers. Additionally, the clipped materials were oven-dried, weighed and preserved for subsequent crude protein and in vitro true digestibility evaluations. These materials were also evaluated for total biomass, total digestible dry matter and total nitrogen yield on a per-hectare basis.

More suckers died over the winter in plots that were clipped in late summer than those clipped in early summer. However, in the first growing season, clipping in early summer resulted in death of more suckers compared to mid- and late summer clipping, but no such difference was noted between seasons for the second year. More suckers died in the first growing season regardless of the clipping intensities compared to the control, but no difference was noted between the control and the clipping intensities in the second growing season. By the end of the second growing season fewer suckers were

present for late summer treated plots (20,444 suckers/ha) than for early summer treated plots (34,944 suckers/ha).

One year after early summer clipping, sucker height growth was restricted at all intensities of clipping compared to the control. However, clipping at intensities 20% and 40% in mid- and late summer did not significantly affect sucker height growth compared to the control. Suckers clipped at 60% intensity in mid- and late summer were limited in height growth by the next clipping cycle.

Leader length for suckers clipped in early summer was not affected differently by intensity of clipping, one year after clipping. For mid- and late summer clipped plots, leader length was more than for the control suckers by the next clipping cycle in year two. Despite having been clipped earlier during the growing season, on average, leader length for suckers clipped at 20% and 40% was not different from the control suckers by the study's end. However, for suckers heavily clipped (60%), leader length was on average shorter than the controls by the end of the study.

Intensity and season of clipping affected twig and bud density on treated suckers. On average, there were fewer twigs on clipped suckers than on the control suckers in the second year, with a tendency to decrease with increasing clipping intensity. In the second year, there were more twigs in early summer treated plots than they were in mid- and late summer treated plots. Similarly, bud density tracked the pattern displayed by twig density.

Basal area of suckers treated in early summer was lower than for mid- and late summer treated plots in year one. By the beginning of the growing seasons in year two, basal area growth for all seasons of clipping were not different. But, by the study's end

basal area growth for suckers clipped in early summer was significantly higher than for late summer treated plots.

Generally, crude protein content of harvested materials decreased as the season progressed and as the intensity of clipping increased. Crude protein ranged from 12.8% to 22.9% and 10.6% to 16.5% in 2006 and 2007, respectively. Harvested materials were highly digestible for all seasons and intensities of clipping, with in vitro true digestibility values ranging from 80.1% to 93.4% and 75.2% to 90.7% in 2006 and 2007, respectively. Biomass (34 kg/ha), total digestible dry matter (31 kg/ha) and total nitrogen (1.1 kg/ha) harvested were lower in early summer than for mid- (181, 142, and 5 kg/ha, respectively) and late (217, 178, and 4.6 kg/ha, respectively) summer in 2006. In 2007, biomass harvested in early summer (139 kg/ha) was lower than for mid-summer (260 kg/ha) season.

Conclusions

Browsing aspen suckers at intensities $\leq 40\%$ in mid- and late summer would ensure that suckers continue to grow normally as the unbrowsed suckers. Because early summer browsing limits sucker height growth, browsing in early summer should not be allowed. Suckers clipped in early summer demonstrated far much reduced sucker height, such that it may take many years before suckers escape the browse zone. As a result, suckers may remain within reach of browsers for many years (more than five years) and thus remain prone to repeated browsing. It is crucial that a clear-felled aspen stand should be managed (to control browsing) until the sucker heights are at least 1.5 m tall.

This management may take about five years before the suckers grow out of reach of browsers.

Nutritionally, browsing suckers at intensities 20% and 40% in mid-summer would provide browsers with crude protein content ranging from 18.1% to 19.2% and 12.8% to 13.5% in the first year and second year of growth, respectively. Additionally, browsing at these tolerable levels can potentially provide digestible dry matter ranging from 84 kg/ha to 102 kg/ha and 164 kg/ha to 198 kg/ha in the first year and second year of growth, respectively.

From an aspen restoration standpoint, designing grazing programs that ensure delayed use for at least the first two months of the growing season the year following clear-felling would ensure aspen stand development and growth. Additionally, it is recommended that a protocol be developed to monitor the responses of suckers to browsing for at least five growing seasons on recently treated pastures.

Research Limitations

Because of the uncertainty on the responses of suckers due to unclipped neighbors, I suggest further (1) research involving actual livestock browsing. Schier (1972) observed that removal of newly initiated suckers from root sections resulted in a greater number of suckers initiating than without removal, suggesting that apical dominance may have been exerted on clipped suckers by the unclipped suckers in the surroundings. As a result, this may have down-played the responses of suckers in my treatments to the clipping intensities. In contrast, Eliason (1971) found that the earliest developing suckers did not appear to inhibit the initiation of other suckers at the base of

growing suckers. (2) As studies have shown, aspen is one of the most genetically diverse trees in North America. My study was not able to address the genetic aspect of aspen and how genetics interact with browsing and season of browsing. Therefore, further research should be undertaken in this regard, especially under natural conditions. (3) Additionally, this study was limited because I had only two years of data. Because the years when treatments were implemented were fairly wet years, additional years of repeated clipping under variable weather conditions would potentially provide a better picture on the responses of suckers. Climatic factors such as periods of wet or dry years may influence the responses by suckers differently compared to what was observed in this study. Since the treatment plots are still in place, I recommend continued clipping and monitoring on the sucker responses for the next three years. (4) Because the digestibility values observed in this study were on the high side (as reported in the literature), I suggest further analysis for the harvested materials using the procedure of Tilley and Terry (1963) to compare the results. (5) Increased levels ($> 60\%$) of clipping may have impacted suckers negatively, resulting in lower sucker densities that are unsustainable with regard to the recommendations of Bartos and Campbell (1998a). Thus, research involving one or more additional intense clipping levels is suggested to determine the level of clipping that is unsustainable in terms of stand density. (6) Lastly, because my study did not cover a large geographic area, I recommend further research covering a wide range of areas across the West.

Overall, my study should serve as a model to develop other research designs going forward on the effects of intensity and season on browsing aspen suckers.

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APPENDICES

APPENDIX A. Map

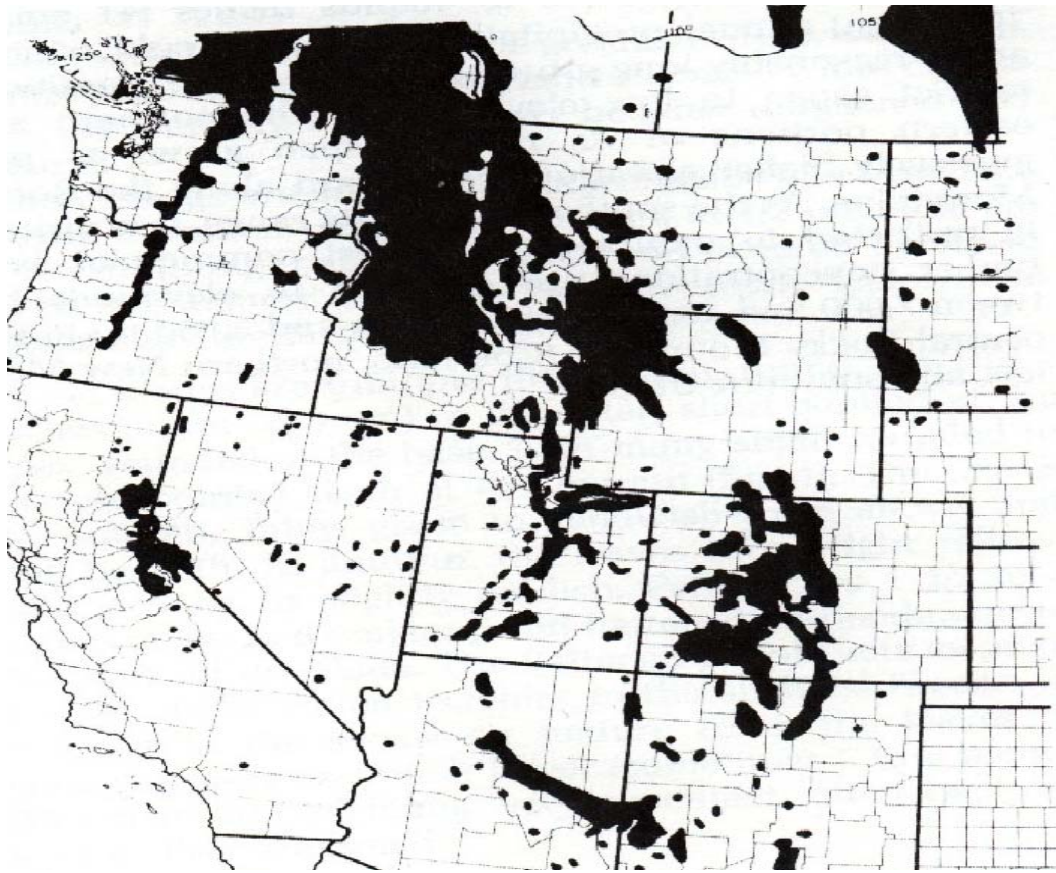


Figure A. The range of aspen in the conterminous western United States. Reproduced from Little (1971).

APPENDIX B. Photographs



Figure B.1. Photograph showing the newly clear-felling-coppice operation for one of the study sites.



Figure B.2. Perimeter fence showing the contrasting browsing regimes inside and outside the exclosure. See how heavily browsed the suckers are at the bottom left corner of the photograph (as shown by the arrow).



Figure B.3. Photograph showing a regeneration of aspen suckers inside the enclosure after clear-felling operation.

APPENDIX C. Tables

Table C.1. Soil textural classes and particle size distributions for study sites on Cedar Mountain, Utah.

Site ¹	Soil texture	Sand	Silt	Clay
		-----%		
1	Sandy-loam	70	20	10
1	Sandy-loam	70	20	10
1	Sandy-loam	69	21	10
1	Sandy-loam	70	18	12
2	Loam/Clay-loam	32	41	27
2	Loam	37	41	22
2	Loam	34	40	26
2	Clay-loam	24	45	31
3	Clay-loam	28	44	28
3	Clay-loam	26	46	28
3	Clay-loam	27	45	28
3	Loam/Clay-loam	30	43	27

¹Four samples were collected from each site.

Table C.2. Soil moisture content (%) for study sites sampled at three seasons in 2007.

Season	Depth (cm)	Water Content (%)	SE ¹
Early summer	15	9.43	1.39
	30	9.55	
Mid-summer	15	5.58	
	30	4.56	
Late summer	15	3.33	
	30	3.33	

¹SE = standard error.

Table C.3. Deoxyribonucleic acid (DNA) extraction results for samples of aspen leaves collected at the three sites.

Sample	Allele 1	Allele 2	Allele 3	Allele 1	Allele 2	Allele 3	Allele 1	Allele 2
1	210	224		119	122		156	169
2	210	224		119	122		156	169
3	210	224		119	122		156	169
4	210	224		119	122		156	169
5	210	224		119	122		156	169
6	207	210	224	122			156	163
7	207	210	224	122			156	163
8	207	210	224	122			156	163
9	207	210	224	122			156	163
10	210	213		119	122		156	169
11	210	213	224	119	122		156	163
12	210	213	224	119	122		156	163
13	213	230		119	122	128	162	169
14	210	213	224	119	122		156	163
15	210	213	224	119	122		156	163

1-5, 6-10, and 11-15 = samples from site 1, 2, and 3, respectively.

Table C.3. -continued

Sample	Allele 3	Allele 1	Allele 2	Allele 3	Allele 1	Allele 2	Allele 3
1		99	101		184	193	
2		99	101		184	193	
3		99	101		184	193	
4		99	101		184	193	
5		99	101		184	193	
6	169	99	115		184	193	196
7	169	99	115		184	193	196
8	169	99	115		184	193	196
9	169	99	115		184	193	196
10		95	101	115	184	193	196
11		97	99		193	196	
12		97	99		193	196	
13		99	103		184	193	
14		97	99		193	196	
15		97	99		193	196	

1-5, 6-10, and 11-15 = samples from site 1, 2, and 3, respectively.

Table C.4. Regression equations for basal diameter (cm) and biomass (g) for the different seasons in 2006 and 2007.

Year	Season	Regression equation	R ²	n
2006	Early summer	$\ln^a y = 2.83 + 2.32 \ln^b x$	0.83	50
	Mid-summer	$\ln y = 3.12 + 2.90 \ln x$	0.89	50
	Late summer	$\ln y = 3.20 + 2.22 \ln x$	0.90	50
	^c October: Whole plant	$\ln y = 2.86 + 2.66 \ln x$	0.89	50
	¹ Twigs	$\ln y = 2.29 + 2.58 \ln x$	0.65	50
2007	Early summer	$\ln y = 2.81 + 2.31 \ln x$	0.76	50
	Mid-summer	$\ln y = 3.07 + 2.52 \ln x$	0.90	50
	Late summer	$\ln y = 2.92 + 2.35 \ln x$	0.77	50
	¹ October	$\ln y = 1.75 + 2.00 \ln x$	0.37	50

^{a,b}Indicate biomass, and basal diameter, respectively.

^cIndicate whole plant biomass and basal diameters were used to develop the regression equation at the end of the growing season. Because suckers in 2006 had emerged in spring and summer that year, whole plant biomass was used in developing the regression equation. ¹However, for the re-growth, basal diameter and biomass of twigs were used instead.

Table C.5. Mean initial current year biomass production (kg/ha) for aspen suckers at the beginning of seasons in 2006 and 2007 on Cedar Mountain, Utah.

Year	Season	Intensity (%)	Biomass (kg/ha)	¹ SE
2006	Early Summer	0	177.6	83.75
		20	190.8	
		40	215.4	
		60	164.9	
	Mid-Summer	0	322.3	83.75
		20	529.5	
		40	433.5	
		60	668.3	
	Late Summer	0	462.6	83.75
		20	824.4	
		40	536.7	
		60	575.5	
2007	Early Summer	0	1196.1	414.59
		20	925.1	
		40	1037.1	
		60	1035.6	
	Mid-Summer	0	987.1	414.59
		20	1807.4	
		40	852.2	
		60	1370.4	
	Late Summer	0	792.8	414.59
		20	1950.4	
		40	1045.6	
		60	717.6	

¹SE indicates standard error.

APPENDIX D. Statistical Programming Codes

SAS Code for the Model for Analysis of Variance for Sucker Variables

Include SAS macro PDMIX800, available at

<http://animalscience.ag.utk.edu/faculty/saxton/pdmix800.sas>

Replace C:\WORK FILES\SAS RESOURCES in the %INCLUDE statement with the appropriate location on your computer.

See comments within PDMIX800.SAS for documentation and citation.

PDMIX800 uses IML, so IML must be installed on your computer.

Note that critical values (e.g., LSDs) are reported in the LOG window!

```
%include 'F:\KOKETSO TSHIRELETSO DISSERTATION DOCUMENTS\PROJECT
SAS CODE\pdmix800.sas';
```

```
PROC IMPORT OUT= KKproject
    DATAFILE= "F:\koketso Tshireletso dissertation documents\dissertation
data\proj_kk1 A"
    DBMS=EXCEL2000 REPLACE;
    GETNAMES=YES;
RUN;
```

```
proc contents data=KKproject varnum;
run;
proc freq data=KKproject;
    table timenumeric -- later_ns ;
run;
```

```
title 'Before clipping measurements data in both years';
data BLUE;
    set kkproject;
    *IF timeNumeric=1; * Alternative subsetting statement;
    if time in ('B06', 'B07');
run;
```

```
proc print data=blue;
run;
```

```
proc sort data=blue;
    by site season treatment time;
run;
```

```
proc means data=blue noprint;
    by site season treatment time;
    var suckerHt;
    output out=suckerHt_Means mean=suckerHt;
run;
```

```
proc print data=suckerHt_Means;
run;
```

```
data suckerHt_Means;
  set suckerHt_Means;
  *logsuckerHt = log(suckerHt);
run;
```

Title 'Model fitting';

```
proc datasets nolist;
  delete lsmeans solutionr diffs mix_out;
run;
proc mixed data=suckerHt_Means covtest cl nobound;
  ods output lsmeans=lsmeans solutionr=solutionr diffs=diffs;
  ods exclude solutionr diffs;
  class site season treatment time;
  model suckerHt = season|treatment|time / ddfm=kr outp=mix_out;
  random site / solution;
  random site*season / solution;
  random treatment*site*season / solution;
  lsmeans season|treatment|time / pdiff adjust=tukey;
run;
```

```
/*      Define macro variables: replace _ with pertinent variables
NOTE that many of these macro variables are case-sensitive
and MUST match the variable names (uppercase, lowercase, any
truncation) in the datasets!
This is set up for a three-way factorial (fixed effects factors)
with three variance components (random effects factors, e.g.,
block, whole plot, subplot) in addition to residual; add or
delete factors as need be. */
%let factor1= Season; /* Fixed effects factor 1 */
%let factor2= Treatment; /* Fixed effects factor 2 */
%let factor3= Time; /* Fixed effects factor 3 */
%let effect12 = Season*Treatment; /* Interaction of factors 1 and 2 */
%let effect13 = Season*Time; /* Interaction of factors 1 and 3 */
%let effect23 = Treatment*Time; /* Interaction of factors 2 and 3 */
%let effect123 = Season*Treatment*Time; /* Interaction of factors 1 and 2 */
%let level1= Site; /* Random effects factor 1 */
%let level2= Site*Season; /* Random effects factor 2 */
%let level3= Site*Season*Treatment; /* Random effects factor 3 */
/*      Create a new dataset with LSMEANS information to plot
+/- SE */
```

```

data lsmeans;
    set lsmeans;
    hi = estimate + stderr;
    lo = estimate - stderr;
    run;
data lsmeans2;
    set lsmeans;
    y=hi; output;
    y=lo; output;
    run;
/*      Plot interactions */
goptions reset=symbol;
proc gplot data=lsmeans2(where=(effect="&effect12"));
    title2 "&factor1 by &factor2 Interaction";
    symbol i=hilojt;
    plot y*&factor2=&factor1;
    run;
proc gplot data=lsmeans2(where=(effect="&effect13"));
    title2 "&factor1 by &factor3 Interaction";
    symbol i=hilojt;
    plot y*&factor3=&factor1;
    run;
proc gplot data=lsmeans2(where=(effect="&effect23"));
    title2 "&factor2 by &factor3 Interaction";
    symbol i=hilojt;
    plot y*&factor2=&factor3;
    run;
proc sort data=lsmeans2;
    by &factor3;
proc gplot data=lsmeans2(where=(effect="&effect123")) uniform;
    title2 "&factor1 by &factor2 by &factor3 Interaction";
    by &factor3;
    symbol i=hilojt;
    plot y*&factor1=&factor2;
    run;
proc sort data=lsmeans2;
    by &factor2;
proc gplot data=lsmeans2(where=(effect="&effect123")) uniform;
    title2 "&factor1 by &factor2 by &factor3 Interaction";
    by &factor2;
    symbol i=hilojt;
    plot y*&factor1=&factor3;
    run;
goptions reset=symbol;
/*      Assess model assumptions */

```



```

/*      Level 1 variance */
proc univariate data=solutionR(where=(effect="&level1")) noprint;
    title2 "&level1 variance";
    probplot estimate / normal (mu=est sigma=est);
    histogram estimate / normal;
run;

/*      Level 2 variance */
proc univariate data=solutionR(where=(effect="&level2")) noprint;
    title2 "&level2 variance";
    probplot estimate / normal (mu=est sigma=est);
    histogram estimate / normal;
run;

/*      Include &factors as appropriate, i.e., those factor(s) for
      which LEVEL2 is the experimental unit */
proc sort data=solutionR;
    by &factor1;
proc boxplot data=solutionR(where=(effect="&level2"));
    plot estimate*&factor1 / boxstyle=schematic;
run;

/*      Level 3 variance */
proc univariate data=solutionR(where=(effect="&level3")) noprint;
    title2 "&level3 variance";
    probplot estimate / normal (mu=est sigma=est);
    histogram estimate / normal;
run;

proc sort data=solutionR;
    by &factor2;
proc boxplot data=solutionR(where=(effect="&level3"));
    plot estimate*&factor2 / boxstyle=schematic;
run;

/*      Residual variance */
proc univariate data=mix_out plot normal noprint;
    title2 'Residual variance';
    probplot resid / normal (mu=est sigma=est);
    histogram resid / normal;
run;

/*      Include &factors as appropriate */
proc sort data=mix_out;
    by &factor1;
proc boxplot data=mix_out;
    plot resid*&factor1 / boxstyle=schematic;
run;

proc sort data=mix_out;
    by &factor2;
proc boxplot data=mix_out;

```

```
        title3;  
        plot resid*&factor2 / boxstyle=schematic;  
        run;  
proc sort data=mix_out;  
    by &factor3;  
proc boxplot data=mix_out;  
    title3;  
    plot resid*&factor3 / boxstyle=schematic;  
    run;  
proc sort data=mix_out;  
    by pred;  
proc gplot data=mix_out;  
    symbol i=none v=plus;  
    plot resid*pred / vref=0;  
    run;
```

APPENDIX E. Plant Data Responses

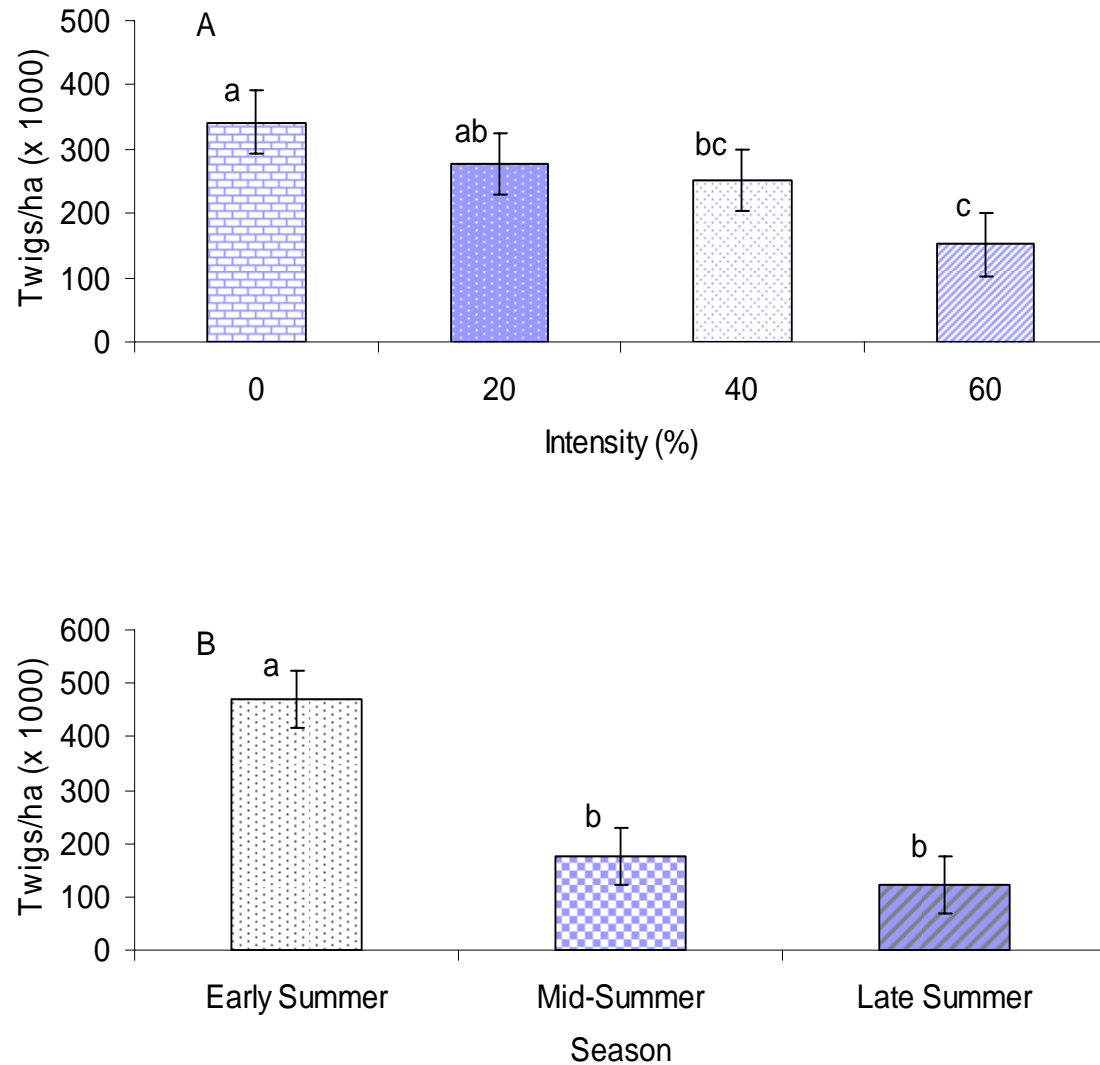


Figure E.1. Effect of clipping intensity (A), and season of clipping (B) on mean twig density of suckers clipped once during their first year of growth. The twig numbers for the three seasons were averaged over B06 and B07 sampling times. B06, B07 = before suckers were clipped at the beginning of seasons in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

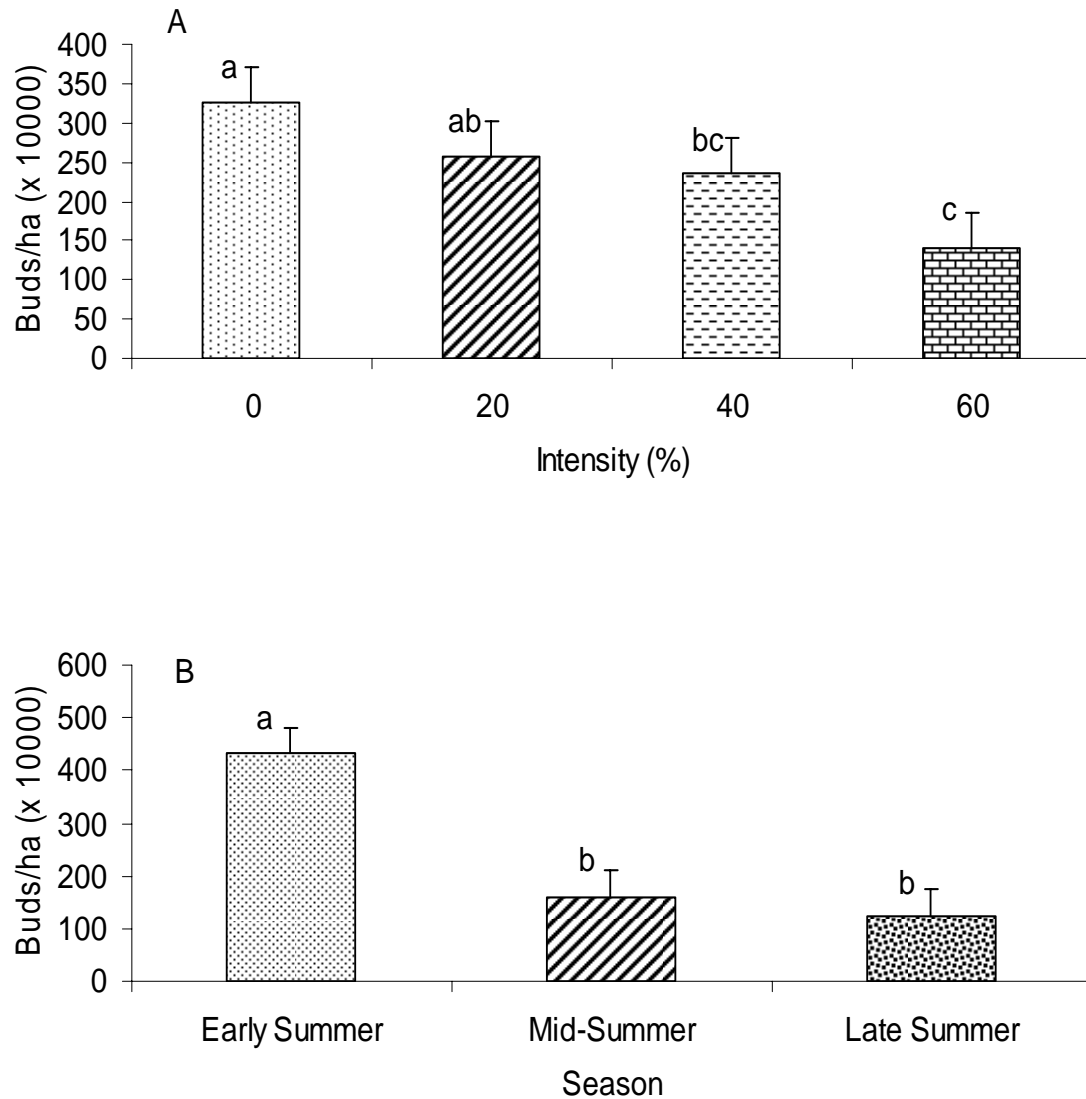


Figure E.2. Effect of clipping intensity (A), and season of clipping (B) on mean bud density of suckers clipped once during their first year of growth. The bud numbers for the three seasons were averaged over B06 and B07 sampling times. B06, B07 = before suckers were clipped at the beginning of seasons in 2006, and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

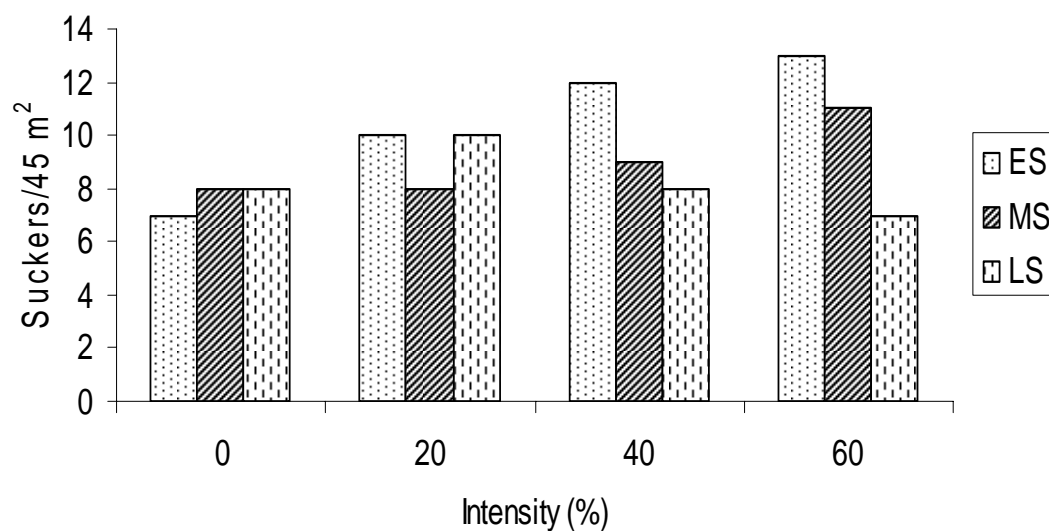


Figure E.3. Total number of new suckers (in all plots for the three stands) that emerged after treatments were implemented shown under each intensity and season of clipping. These suckers were noted in the summer of 2007. ES, MS, LS = early-, mid- and late summer, respectively.

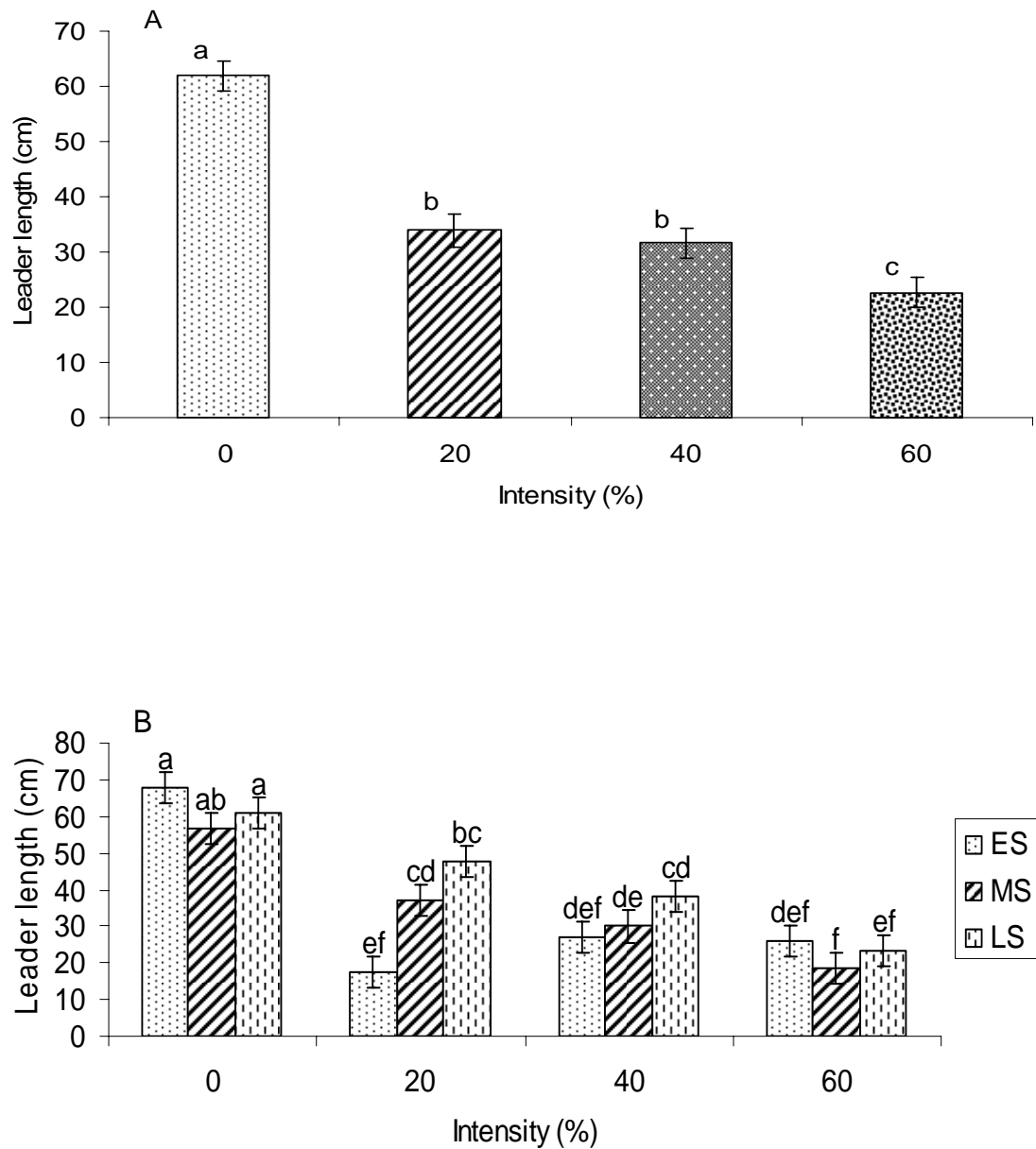


Figure E.4. Effect of clipping intensity (A) and season and intensity (B) on mean leader length of suckers clipped twice during their life. The leader length for the intensities were averaged over A06 and A07 sampling times. A06, A07 = end of the growing season in 2006 and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

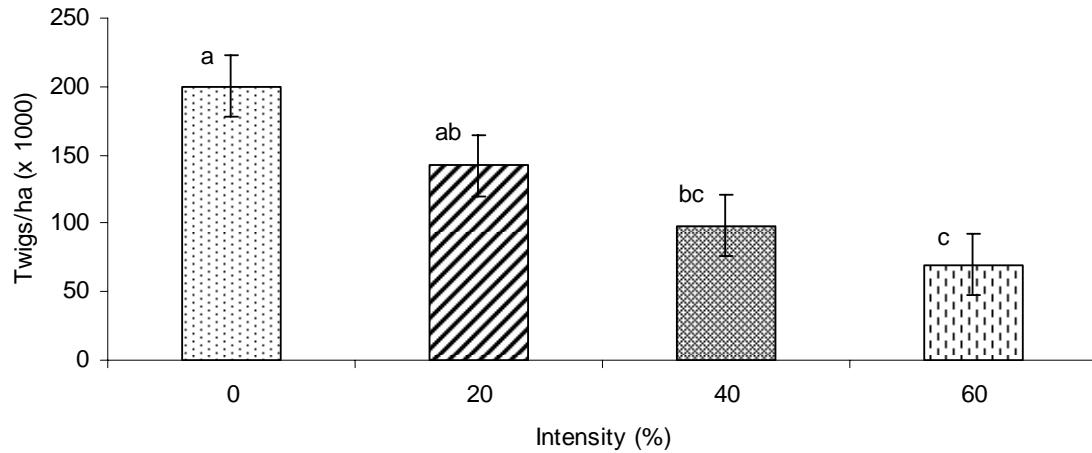


Figure E.5. Effect of clipping intensity on mean twig density of suckers clipped twice during their life. Twig density for the different intensities were averaged over A06 and A07 sampling times. A06, A07 = end of the growing season in 2006 and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

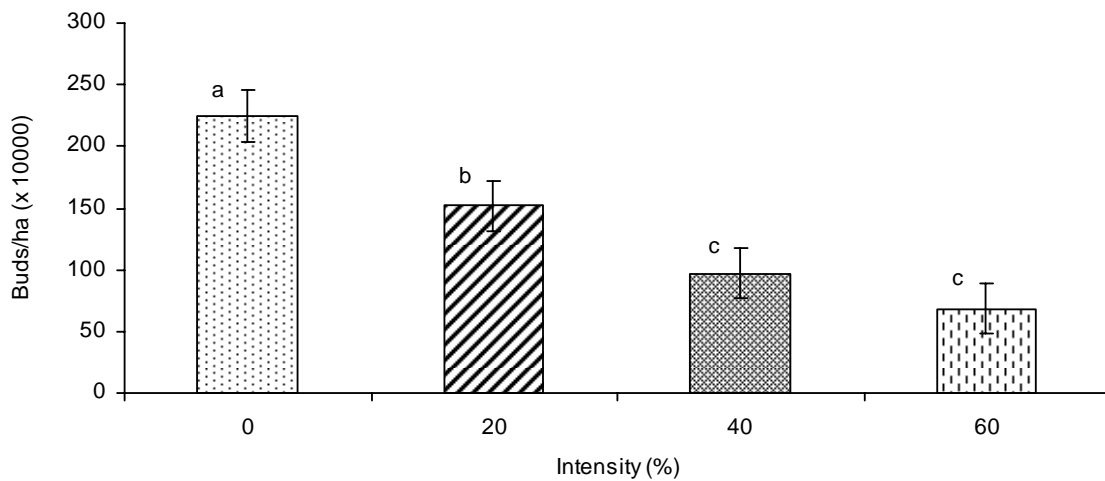


Figure E.6. Effect of clipping intensity on mean bud density of suckers clipped twice during their life. Bud density for the different intensities were averaged over A06 and A07 sampling times. A06, A07 = end of the growing season in 2006 and 2007, respectively. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

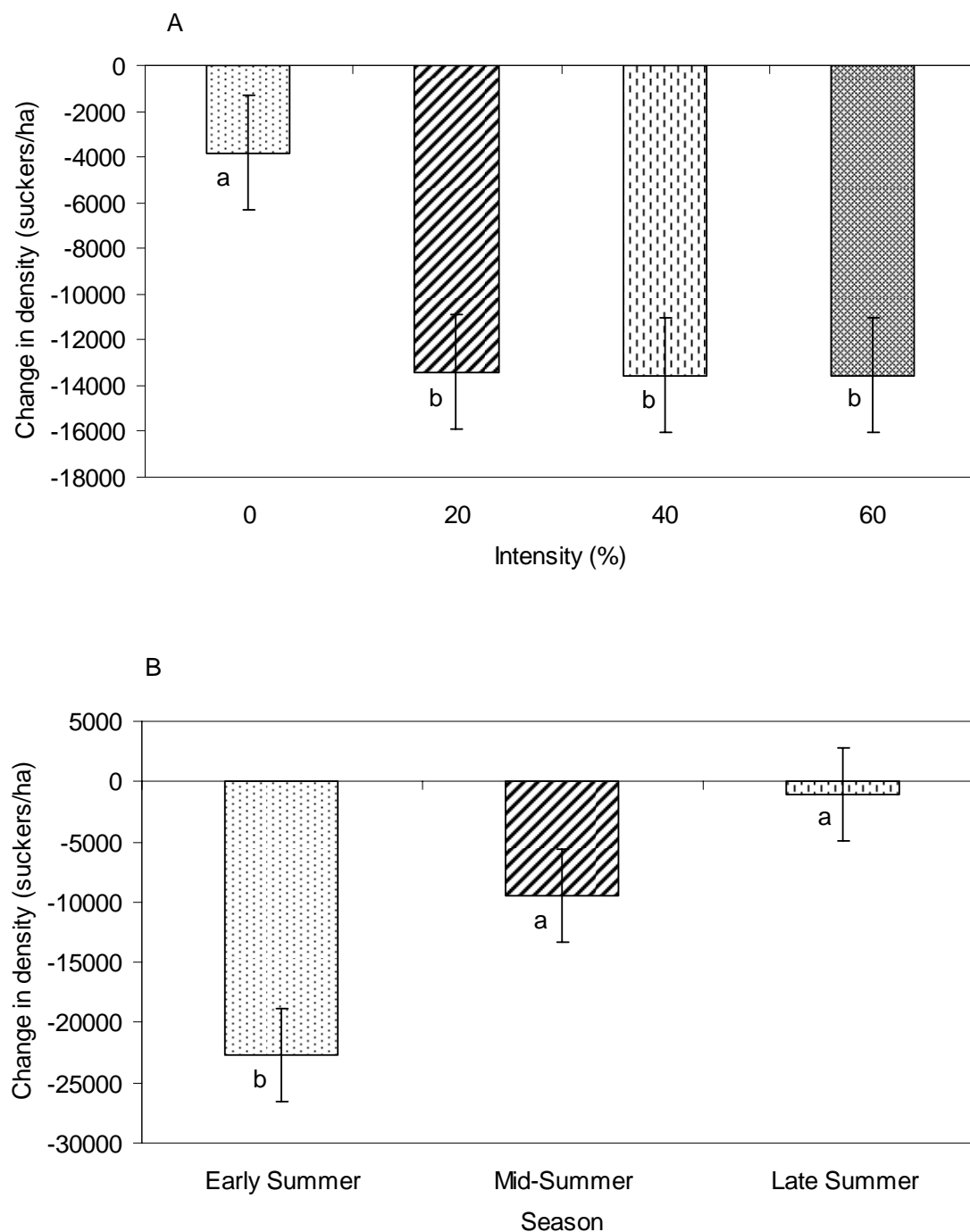


Figure E.7. The effect of clipping intensity (A), and season of clipping (B) on mean sucker density changes averaged over 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

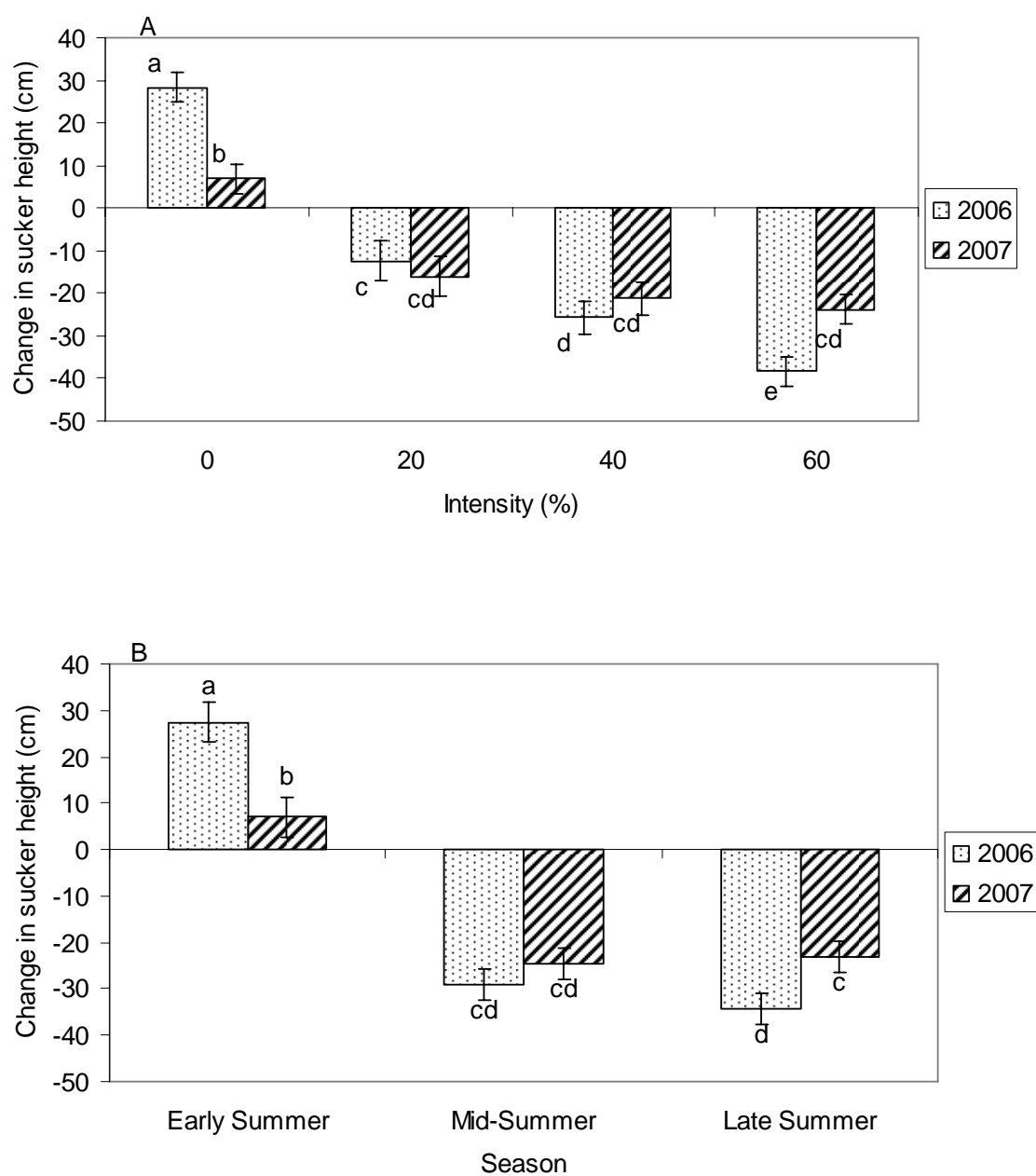


Figure E.8. The effect of clipping intensity (A), and season of clipping (B) on mean sucker height changes averaged over 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

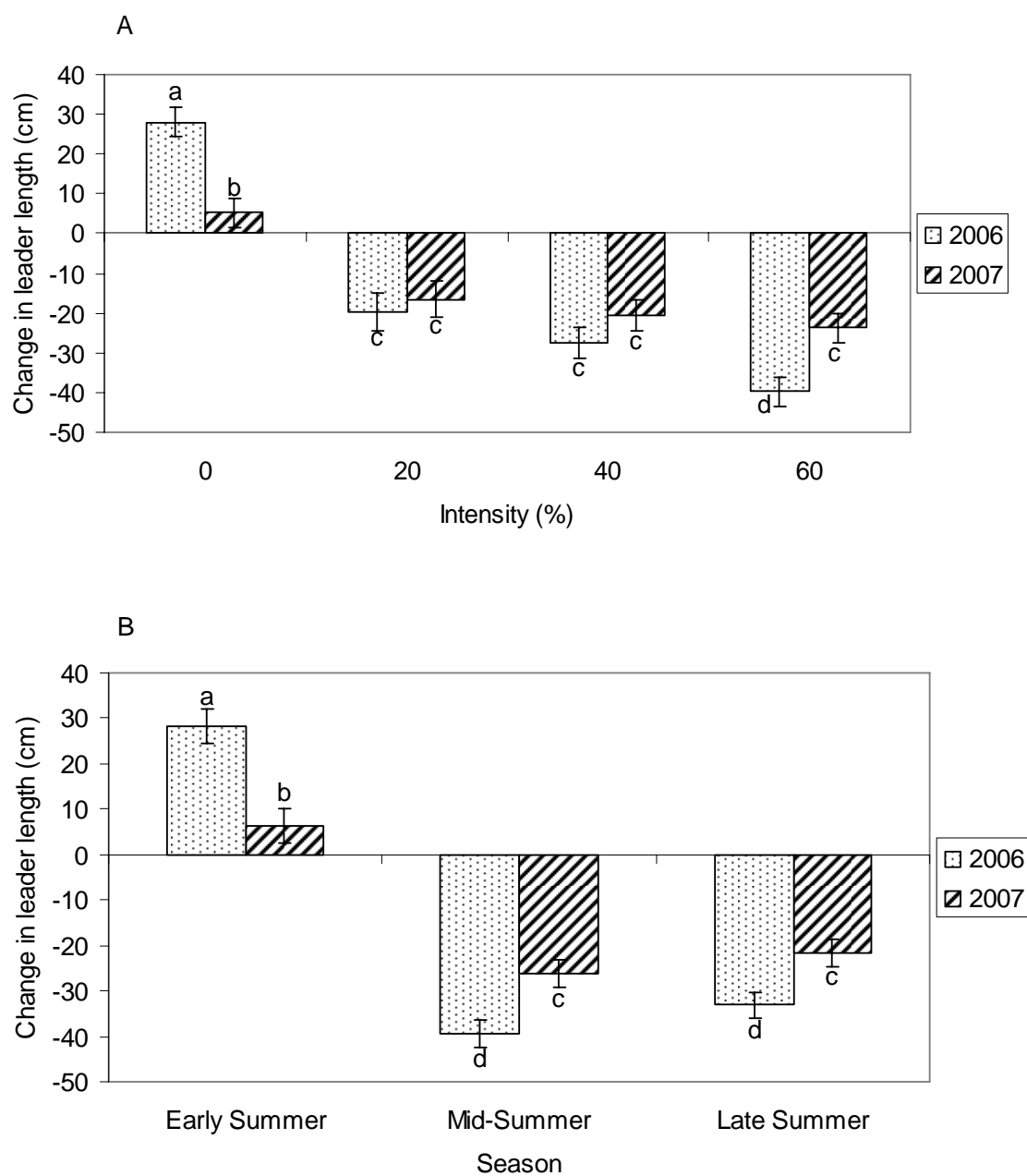


Figure E.9. The effect of clipping intensity (A), and season of clipping (B) on mean leader length changes averaged over 2006 and 2007. Bars indicate standard errors. Means with different letters are significantly different at $P < 0.05$.

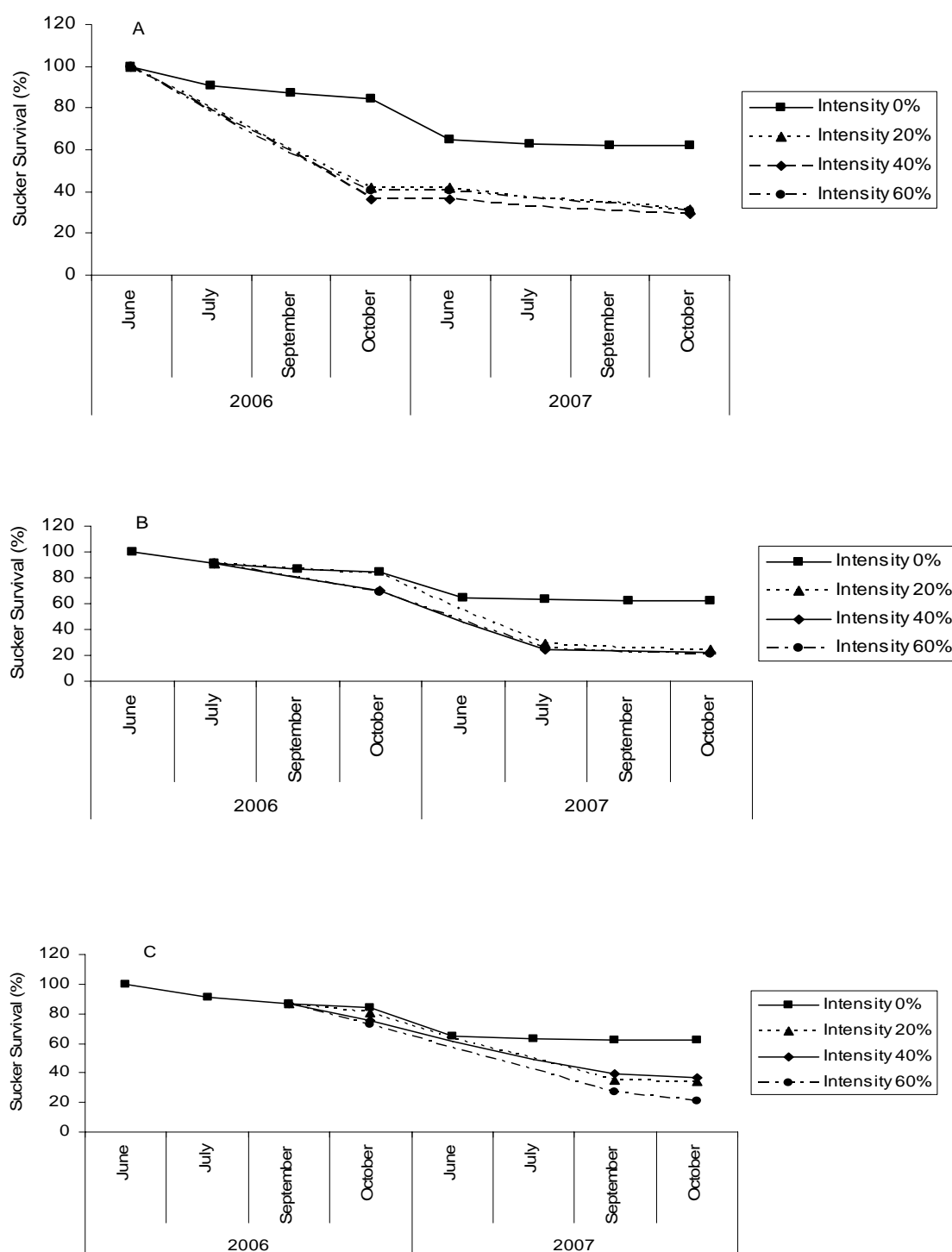


Figure E.10. Sucker survival of (A) early summer, (B) mid-summer and (C) late summer treated plots through the summer growing season in 2006 and 2007.

CURRICULUM VITAE

Koketso Tshireletso
(February 2008)

PERSONAL INFORMATION:

Born March 6, 1971 at Gweta village, Central District of Botswana. Son of
Jenamo Tshireletso and Tshireletso Baageleng.

CAREER OBJECTIVE:

To continue lecturing at University of Botswana, Botswana College of
Agriculture, Gaborone, Botswana; hope to be involved in research that includes
among other things, rangeland policy, plant-animal interactions, physiology of
range plants, disturbance ecology (e.g. fire effects on rangelands).

EDUCATION:

BS in Agriculture, University of Botswana, Gaborone, Botswana. (5/96) (2 i ≈ A)
Emphasis in Animal Science, Crop Science, Agricultural Engineering Science,
Agricultural Economics and Extension. MS in Range Science, New Mexico State
University, Las Cruces, New Mexico. (8/01) Grad GPA: 3.667 (4.0 = A)
Emphasis in Range Management. PhD in Range Science, Utah State University,
Logan, Utah. (expected 5/08). Grad GPA: 3.67. Dissertation research conducted
at Cedar Mountain, Utah 2005-2007.

EXPERIENCE:

Teaching: Taught at Kelemogile Community Junior Secondary School,
Ramotswa, Botswana, from September 1996 to April 1997; taught at Botswana
College of Botswana (BCA), University of Botswana, between 1997 and 2004.

Courses included Range Survey and Monitoring, Animal Nutrition and Range Science, Introductory Range Science, Rangeland Ecology and Range Management.

Other assignments: Grading research projects for diploma students at Botswana College of Agriculture, University of Botswana, Botswana.

RESEARCH AND PUBLICATIONS:

Journal Articles:

Omphile, U. J., A. A. Aganga, K. Tshireletso, and R. Nkele. 2004. Foraging strategies of sheep and goats under semi-intensive management in Botswana. *South African Journal of Animal Science* 34:120-122.

Aganga, A. A., T. Adogla-Bessa, U. J. Omphile, and K. Tshireletso. 2000. Significance of browses in the nutrition of Tswana goats. *Archivos de Zootecnia* 49:469-480.

Conference Proceedings:

Aganga, A. A., O. R. Madibela, U. J. Omphile, K. Tshireletso, and P. Kgwalalala. 2006. Farmer's knowledge in the utilization of indigenous browse species for feeding livestock in Kweneng District of Botswana. Proceedings of the British Society of Animal Science. Published by the British Society of Animal Science. ISBN 0906562 52X.

Tshireletso, K., R. F. Beck, and R. McNeely. 2001. The effects of drought with grazing on perennial grass response in Northern Chihuahuan Desert. A poster presentation at the Jornada Experimental Range Agricultural

Research Annual Symposium held in July 2001 at New Mexico State University, Las Cruces, New Mexico, USA.

Aganga, A. A., K. Tshireletso, and M. Mathaio. 1999. Assessment of the chemical composition of some locally available browse seeds as ruminant feed in Botswana. *In*: A. A. Aganga [ED.]. Proceedings of the sheep and goats workshop held at the Centre of In-service and Continuing Education; 19-23 April 1999; Gaborone, Botswana, Africa: Enhancing sheep and goats production in Botswana. p. 35-46.

Aganga, A. A., and K. Tshireletso. 1999. Nutrient recycling: Use of broiler litter as protein supplement for Tswana sheep and goats. *In*: A. A. Aganga [ED.]. Proceedings of the sheep and goats workshop held at the Centre of In-service and Continuing Education; 19-23 April 1999; Gaborone, Botswana, Africa: Enhancing sheep and goats production in Botswana. p. 67-78.

Aganga, A. A., K. Tshireletso, and M. S. Mathaio. 1999. Quality assessment of *Albizia amara*, *Albizia harveyi*, *Acacia burkei*, *Bolusanthus speciosus*, *Ochna pulchra* and *Sterculia africana* seeds as animal feed. 8th Napreca. International symposium on natural products; 9–13 August 1999; University of Botswana, Gaborone, Botswana: Book of extended abstracts. p 41–44.

Other Research Efforts:

Involved in a number of Research Projects with other colleagues at Botswana College of Agriculture, Botswana. These projects include “Diet Selection and influence of Tannin Containing Browsers in the Nutrition of Tswana Goats” and “Desert Margin Project: Utilization of key forage plants in two desert margin areas of Botswana”. These projects are on-going.

Thesis:

Tshireletso, K. 2001. The effects of drought on plant response in Northern Chihuahuan Desert rangelands [thesis]. Las Cruces, NM, USA: New Mexico State University. 100 p.

Tshireletso, K. 1996. Yield and quality of two grasses over-sown with a legume [B.Sc thesis]. Gaborone, Botswana: University of Botswana. 27 p.

SERVICE:

Service to University of Botswana: Member of the University of Botswana Graduation Committee from 1998 to 1999.

Service to Botswana College of Agriculture: Member of the Gender and Graduate Prize Committees from 2002 to 2003; advisor to the Botswana College of Agriculture Environmental Club from 1998 to 2004; represented BCA (Animal Science Department) at a National Workshop on Food Industry, held at Gaborone Sun, Botswana, on 18-19th August, organized by Botswana Technology Center in 1998; served as Hostel Warden from 1997 to 1999 at BCA; represented the ASP

department as a member of the organizing committee for CSP Workshop on Crop Production in the 21st Century: Prospects and Challenges for Botswana, held at Centre for In-service and Continuing Education (CICE), Gaborone. Botswana.

Community Service: Visited Red Cross in Tlokweng with BCA Environmental Club and helped put up shade structures for vegetables in October 2003; helped in National Parks and Game Reserves with BCA Environmental Club to put up road signs to aid guide tourists visiting these wildlife conservation areas in 1998, 1999 and 2002.

Other Information: Attended a training of trainer's (TOT) course on "Food Security and Poverty Alleviation" organized and sponsored by Southern African Development Coordinating Conference (SADCC) from 5 September to 30 November 2001 at the Institute of Administration and Commerce (IDM), Gaborone, Botswana; attended a course on livestock judging on 14–18 June 1999 held at Centre for In-service and Continuing Education, Botswana College of Agriculture. Sebele. Gaborone. Botswana; attended a one week course on beekeeping (15-19 April 1991) while on Tirelo Setshaba (National Service) at Denman Rural Training Centre (DRTC). Sebele. Gaborone. Botswana, a course organized for Agricultural Technical Officers for the Southeast District to which I was attached.